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Primary bone microanatomy records developmental aspects of life history in catarrhine primates

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ABSTRACT

A central challenge in human origins research is to understand how evolution has shaped modern human life history. As fossilized remains of our ancestors provide the only direct evidence for life history evolution, efforts to reconstruct life history in paleontological contexts have focused on hard tissues, particularly on dental development. However, among investigators of other vertebrate groups, there is a long tradition of examining primary bone microstructure to decipher growth rates and maturational timing, based on an empirical relationship between the microanatomy of primary bone and the rate at which it is deposited. We examined ontogenetic variation in primary bone microstructure at the midshaft femur of *Chlorocebus aethiops*, *Hylobates lar*, and *Pan troglodytes* to test whether tissue type proportions vary in accordance with predictions based on body mass growth patterns described previously. In all taxa, younger age classes were characterized by significantly higher percent areas of fibro-lamellar and/or parallel-fibered tissues, while older age classes showed significantly higher proportions of lamellar bone. In prior experimental studies, fibro-lamellar and parallel-fibered tissue types have been associated with faster depositional rates than lamellar bone. Principal components analysis revealed differences among taxa in the timing of this transition, and in the particular tissue types observed among individuals of similar dental emergence status. Among M1 and M2 age classes, higher proportions of parallel-fibered and fibro-lamellar tissues were observed in those taxa characterized by reportedly faster body mass growth rates. Further, persistence of fibro-lamellar tissue throughout DECID, M1 and M2 age classes in chimpanzees contrasts with the pattern reported previously for modern humans. Despite the necessary limitations of our cross-sectional study design and the secondary remodeling of bone in primates, large areas of primary bone remain intact and represent a valuable and independent source of information about the evolution of growth and development in the fossil record.

1. Introduction

The study of life history is concerned with those events and developmental processes that occur during the life cycle, and which determine the manner in which organisms allocate energy towards growth, reproduction and maintenance to optimize reproductive effort over their life span (Smith, 1992; Leigh and Blomquist, 2007). Ontogeny has figured prominently in the study of primate life histories, as offspring growth trajectories are governed by energetic trade-offs that determine changes in allocation towards the maturation of different body systems throughout life. Prior work has shown that different anatomical organs/systems (e.g., brain, body, dentition, and reproductive) may be developmentally dissociated from one another, and their growth rates and timing subject to independent selection (Watts, 1990; Leigh and Park, 1998; Bolter and Zihlman, 2003; Pereira and

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Abbreviations

CPL	Circularly polarized light microscopy
DECID	Biological age class defined by alveolar emergence of one or more deciduous teeth
ECC	Compacted coarse cancellous bone; tissue type of endosteal origin
ELAM	Lamellar bone; tissue type of endosteal origin
EPIPH	Biological age class defined on the basis of long bone epiphyseal union
EPF	Parallel-fibered bone; tissue type of endosteal origin
EPF-LAM	Transitional parallel-fibered to lamellar bone; tissue type of endosteal origin
FLC	Fibro-lamellar complex; tissue type of periosteal origin
FLC-LZPO	Transitional fibro-lamellar complex to lamellar-zonal bone; tissue type of periosteal origin
FLC + LZPO	FLC and FLC-LZPO tissue types grouped for statistical analysis
HAV	Haversion bone (i.e., secondary osteonal bone)
LAG	Line of arrested growth
LAM	Lamellar bone; tissue type of periosteal origin
LM	Brightfield microscopy
M1	Biological age class defined by alveolar emergence of one or more first permanent molars
M2	Biological age class defined by alveolar emergence of one or more second permanent molars
M3	Biological age class defined by alveolar emergence of one or more third permanent molars
PF	Parallel-fibered bone; tissue type of periosteal origin
PF-LAM	Transitional parallel-fibered to lamellar bone; tissue type of endosteal origin
SF	Sharpey fiber bone

Leigh, 2003; Godfrey et al., 2004; Leigh and Bernstein, 2006; Dirks and Bowman, 2007). These diverse 'modes' of development underlie important differences in primate life history strategies (Pereira and Leigh, 2003). Shifts in the rate and timing of different body systems, namely dental versus skeletal growth, also characterize fossil hominins, suggesting that modularity may underlie life history evolution in the human lineage (Smith, 1993; Pereira and Leigh, 2003; Dean and Smith, 2009).

A major focus of our efforts to understand how evolution has shaped primate life history strategies has been on hard tissue features observable in fossils. Among investigators of other vertebrate groups, including mammals, there is a long tradition of examining the microscopic organization of primary bone tissues (i.e., those deposited during growth, as opposed to secondary remodeling) in both modern and fossil samples as a means of revealing life history information, including growth rates, maturational timing, and longevity (e.g., Enlow, 1966; Castanet et al., 1993; Ricqlès, 1993; Klevezal, 1996; Padian et al., 2001; Chinsamy-Turan, 2005; Erickson, 2005; Castanet, 2006; Köhler and Moyà-Solà, 2009; Padian, 2013; Kolb et al., 2015). The microscopic organization of bone records a history of its growth and development, and thus represents a potentially rich source of information about the various ontogenetic, environmental, local and phylogenetic factors that influence its formation and maintenance during life (Enlow, 1963, 1966; Ricqlès, 1993; Martin et al., 1998; Currey, 2002; Legendre et al., 2013). Yet, its significance for revealing developmental aspects of life history in primates has been largely unexplored, with a few notable exceptions. The current study begins to address this shortcoming. Identifying shifts in dental development has been critical to our understanding of human life history evolution from evidence available in the fossil record (e.g., Bromage and Dean, 1985; Smith, 1992; Dean, 2010; Schwartz, 2012). However, a foundation based on the incorporation of studies of tooth and bone microanatomy in the same individuals would allow us to more fully address questions concerning developmental modularity and the evolution of other unique human life history traits, such as our slow somatic growth during childhood (Bogin and Smith, 1997; Leigh, 2001; Dean and Smith, 2009; Bromage et al., 2009b).

1.1. *Bone microanatomical diversity*

The cells, vascular canals, and collagen fiber matrix of bone combine to produce stereotypical patterns of microanatomical organization, often referred to as bone 'tissue types'. While bone microanatomy varies along a continuum, investigators have historically used typological classifications to characterize diversity and facilitate comparisons among groups (e.g., Quekett, 1855; Foote, 1916; Amprino and Godina, 1947; Enlow and Brown, 1956; Smith, 1961; Enlow, 1963; Pritchard, 1972; Ricqlès, 1975; Francillon-Vieillot et al., 1990). Figure 1 depicts different tissue types that have been described previously, or are observed here, to occur in primate bone. These tissue types are recognized on the basis of multiple criteria, such as developmental origin, collagen fiber organization, and vascularization (Enlow, 1963, Ricqlès, 1969, 1975, 1977; Francillon-Vieillot et al., 1990; Ricqlès et al., 1991; Enlow and Hans, 1996). (See Supplementary Online Material [SOM] for a more comprehensive description of tissue type diversity as it pertains to the current study.) Bone tissue type distributions vary considerably among vertebrate taxa, individuals of different ages, and within single skeletons (Quekett, 1855; Foote, 1916; Demeter and Mátyás, 1928; Amprino and Godina, 1947; Enlow and Brown, 1956, 1957, 1958; Singh et al., 1974). This diversity can be largely understood as a reflection of ontogenetic, local (e.g., biomechanical), environmental (e.g., nutritional) and phylogenetic factors (Enlow, 1963; Ricqlès, 1993; Martin et al., 1998; Castanet et al., 2001; Currey, 2002; Pearson and Lieberman, 2004; Ricqlès, 2007; Gosman, 2012; Maggiano, 2012).