2. Inferring primate growth, development and life history from dental microstructure: The case of the extinct Malagasy lemur, *Megaladapis*

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Abstract

Teeth grow incrementally and preserve within them a record of that incremental growth in the form of microscopic growth lines. Studying dental development in extinct and extant primates and its relationship to life history and ecological parameters (e.g., diet, somatic growth rates, gestation length, age at weaning) holds the potential to yield unparalleled insights into the life history profiles of fossil primates. In this paper, we use the incremental growth record preserved in teeth to reconstruct dental development, and thereby infer the life history of *Megaladapis edwardsi*, a giant, gorilla-sized, extinct lemur of Madagascar. By examining the microstructure of the first and developing second molars of a juvenile individual, we establish its chronology of molar crown development (M_1 CFT = 1.04 years; M_2 CFT = 1.42 years) and determine its age at death (1.39 years). Crown initiation, formation, and completion times are short compared to *Gorilla*. Microstructural data on prenatal M_1 crown formation time allow us to calculate a minimum gestation length of 0.54 years for *M. edwardsi*, compared to 0.70 years in *Gorilla*. Postnatal crown and root formation in *M. edwardsi* data allow us to estimate the age at M_1 emergence (~0.9 years), and to establish a minimum age for M_2 emergence (>1.39 years).If *Megaladapis* were developmentally similar to large-bodied anthropoids (such as gorillas), we might expect it

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to exhibit slow dental development coupled with relatively early replacement of its deciduous molars. This is not the case. Total molar development is comparatively rapid and poorly explained as a function of adult body mass.

Introduction

Research on the ecomorphology of subfossil lemurs has helped us paint rather detailed pictures of their adaptive profiles (positional behavior, activity rhythms, and even grooming behavior; see Jungers et al., 2002). What has been less forthcoming is information about the life histories of these organisms. Only recently has it been possible to reconstruct important aspects of life history variation in fossil prosimians. Because life histories are "manifestations of ontogenies played out within population contexts" (Godfrey et al., 2002: 114), it is possible to use ontogenetic data to recover aspects of the life history profiles of extinct species. An excellent place to begin is by deciphering the chronology of developing teeth.

Teeth are a unique biological system in that two of their component hard tissues (enamel and dentine) preserve a permanent record of their growth in the form of incremental markings. As a result, direct evidence for the timing of important developmental events during evolution is available from even fragmentary dental remains. Among the developmental hallmarks that can be inferred from the dental growth record are the overall sequence and pace of dental eruption, the timing of first molar emergence, gestation length, and weaning age to name just a few. The timing of each of these events is tightly linked to a primate's overall life history schedule (e.g., Smith, 1991, 2000). Thus, reconstructing the pattern and pace of dental development using incremental markings preserved within dental hard tissues makes it possible to reconstruct the life history of extinct primates with unparalleled accuracy.

As an example of the kinds of life history inferences that can be garnered from the internal growth record of teeth, we provide microstructural data on the incremental lines in extinct lemur teeth to reconstruct the chronology of dental development, tooth emergence, gestation length, and overall life history schedule in one of the largest Malagasy lemurs, *Megaladapis edwardsi*. We also test the correlation between body mass and the overall pace of life history by comparing the pace of dental development and emergence to a range of extant primates, including the similarly-sized *Gorilla gorilla*.

Why Teeth?

A vast literature exists on the basics of tooth growth and histology (see Aiello and Dean, 1990 and Hillson, 1996 for reviews). Essentially, teeth grow incrementally, like trees or shells, and the cells that produce the two main tissue components of tooth crowns (ameloblasts in enamel and odontoblasts in dentine) do so in accordance with the body's circadian rhythm. As these cells secrete enamel and dentine, they leave in their wake a trail of incremental markings, of which there are two types: short-period, or daily, lines (cross striations in enamel, von Ebner lines in dentine), and longer-period lines (striae of Retzius in enamel and Andresen lines in dentine) (Figure 1); see Schwartz and Dean (2000) for a review of tooth growth. These incremental features provide a "road map" for charting the total amount of time, to the day, it takes to form individual tooth crowns (termed crown formation time, CFT) and roots, the timing of tooth initiation for individual teeth, a chronology of dental development for an entire associated dentition, the