

# 1. Introduction

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## Introduction

A decade has past since I last reviewed the various ways in which studies of dental development can contribute to what was then still called hominid paleobiology (Wood, 1996). A little more than eighty years have passed but Adolph Schultz's (1924) seminal contribution is still largely ignored and his paper is seldom cited. Nonetheless, its concluding sentence is worth quoting verbatim once again "With these few and scattered observations on the relation of the growth of the primates to man's evolution...it is hoped to have at least stimulated further investigations and thought – perhaps criticism – in this promising field" (*ibid.*, p. 163). It perhaps took longer than Schultz anticipated for researchers to appreciate the prescience of his prediction and even now we are only just beginning to realize how promising the field of comparative primate growth and development is. Indeed, a decade ago my own appreciation of the potential importance of dental development for improving our understanding of human evolutionary history at many levels was very incomplete.

We hear a good deal about "intelligent design", but for the biologist the dentition is a prime example of "fortunate design". This is because millions of years of evolution have crafted in the form of the dentition a morphological complex that provides opportunities to study both the processes at work in evolution and the patterns that result from those processes. They can be studied at the level of the molecule, the cell, in more than one cell of the same type, in a single tissue, and in more than one tissue in a single tooth (e.g., Shellis, 1984, 1998; Dean et al., 1993; Dean, 1995; Dean and Scandrett, 1996; Antoine et al., 2001; Kangas et al., 2004; Lucas, 2004; Schwartz, 2005). Added to this good fortune is the benefit that in mammals including primates the phenotype of this morphological complex comes in the form of discrete meristic morphological packages called teeth. Individual teeth can be studied at each of the first five levels listed above, as can several teeth of the same tooth type and teeth of more than one type. But a tooth is not an independent entity. The functional potential of a tooth cannot be realized unless it works in concert with other teeth within a functionally integrated

masticatory system (Lucas, 2004) so the hard tissues of the dentition can be studied as an integrated unit and the dentition can be combined with other hard and soft tissues of the masticatory system as an integrated unit. But there is more good fortune. Unlike bone, dental tissues grow in an orderly and incremental fashion and they are not subjected to the remodeling that bedevils attempts to use bone microstructure to recover information about the growth and development of the bony skeleton. Dental microstructure can potentially preserve evidence of the cellular activity involved in the growth and development of teeth in exquisite detail. This potential has been realized, for in some studies the daily activity of single cells has been tracked for hundreds of days. The final piece of good fortune is the fact that teeth are made of the densest tissues in the body. This factor, combined with their compact shape, results in teeth and jaws being particularly well represented in the hominin fossil record.

Until relatively recently, the data extracted from the dental evidence for hominin evolution was essentially limited to variables that described the macrostructure of the crowns of teeth that had completed their ontogeny. These data were either simple linear measurements that described (albeit relatively crudely) the overall size and shape of the crowns of the teeth, or they were non-metrical observations that drew attention to details of the shape of the tooth crowns. The four papers in the Growth and Development section of this volume illustrate some of the ways in which the ontogeny of isolated teeth and of dentitions can help deepen our understanding of human evolution.

If we restrict ourselves to the extant taxa within the African ape clade, we might be tempted to think that there are significant constraints on the relative sizes of the crowns of the anterior (incisors and canine) and posterior (premolars and molars) teeth. Fortunately the hominin fossil record shows us that

these constraints are apparent and not real. The hominin taxa many researchers include within the genus *Paranthropus* are assigned to a separate genus in part because they combine small incisor and canine crowns with massive postcanine crowns. This is not a size-related change because it is a departure from allometric trends within and among Old World primate taxa (Wood and Stack, 1980). This suggests the type of developmental independence that is implied in dental field theories of the type put forward by Butler (1939) and refined by Dahlberg (1945). One of the most significant recent advances in dental science has been the quantitative genetic studies of Leslea Hlusko and colleagues. Their seminal contribution was to realize the importance of (and then very effectively exploit) the resource represented by the *Papio hamadryas* colony at the Southwest National Primate Research Center (SNPRC) in San Antonio. Mating is controlled within the colony and there are meticulous records of the pedigree of these animals. Hlusko and Mahaney (2007) mined this resource (along with a pedigreed mouse colony) to test the independence of linear measurements of incisors and molars (in the mice) and premolars and molars (in the baboons). Their study is preliminary, but the results suggest that incisor and molar size are independent and that premolar and molar size are partially independent.

The second and third of the four papers deal with the timing and the sequence of events in dental development. Monge et al. (2007) base their study on radiographs of 170 children from two dental clinics in Pennsylvania. The chronological age of each child was not estimated from radiographs, but was known from the clinical records. Each radiograph was assessed on the basis of the later stages of  $M_1$  calcification and on  $M_2$  calcification. The study shows that when compared to two "industry standard" reference samples, those of Moorrees et al. (1963) and Demirjian et al. (1973), this contemporary sample of