1. Introduction

B.A. WOOD
The George Washington University
CASHP
Department of Anthropology
2110 G Street, NW
Washington DC 20052, USA
bwood@gwu.edu

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

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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 children from Pennsylvania is developing their teeth earlier. What this shows is that modern human dental developmental schedules are remarkably plastic. The problem it poses is what developmental schedule should be used to represent modern humans when assessing the developmental schedule of a fossil hominin taxon? Monge et al. remind the reader that Zihlman et al. (2004) have already "rattled the bars" of comparative dental developmental studies by showing that wild chimpanzees have longer developmental schedules than the captive chimpanzees whose schedules have heretofore been used as the comparator when assessing the developmental schedules of fossil hominins. Perhaps the developmental schedules of aboriginal populations of modern humans and wild chimpanzees were more similar than the existing comparators suggest? Let us hope that dental clinics for the Hadza and the Ache are set up soon.

Braga and Heuze (2007) use a creditably large (2089 children) data set to explore whether, at least as far as the sequence of dental development is concerned, the whole is simply a sum of its parts, or whether a comprehensive dental developmental schedule contains more information than is contained in the developmental schedules of each tooth or each tooth type? What is the effect, if any, of the interactions between the teeth in the developing mandibular dentition? Can one tooth type, say the anterior teeth, serve as a proxy for the dentition as a whole? The results of their study have implications for the analysis of the dental developmental schedule of fossil hominins for researchers often have to make do with data from just one or two teeth, from which they are tempted to extrapolate to the developmental schedule of the whole dentition. To cut another elegant analytical story short Braga and Heuze suggest that the developmental schedules of tooth types can best be thought of as semi-independent "modules", much like those used for dental morphology. Effectively, they have posted the equivalent of a "health warning" on a packet of cigarettes; anterior teeth should not be used as a proxy for the dentition as a whole, or for other tooth types. Paleoanthropologists take note.

The fourth paper in this series, by Smith et al., focuses on the ontogeny of individual teeth. One of the disadvantages of relying on the morphology of the crown surface for information about taxonomy and phylogeny is that wear soon removes this information. Fortunately just as CT has enabled researchers to capture information about the internal structure of bones (e.g., the temporal bone, see Spoor and Zonneveld, 1998), the relatively recent availability of microCT is enabling researchers to capture morphological information about the internal structure of teeth. MicroCT produces virtual slices through a tooth crown, and enamel and dentine are sufficiently dissimilar structurally and chemically (Schroeder, 1991) that the boundary between the dentine and the enamel can be detected (e.g., Skinner, 2005). With suitable software the images from all the slices through a tooth crown can be integrated to produce a virtual solid rendering of the outer surface of the dentine (DEJ), which is of course the same as the inner surface of the enamel. Smith et al. (2007) go further and suggest that the spatial geometry of the DEJ can be used to reconstruct the order of cusp initiation and coalescence. A previous study had looked at 24 dm_2 germs at different stages of development (Avishai et al., 2004). Within that sample, although the order of cusp initiation was the same, the order in which the cusps coalesced differed. Specifically they found that while the entoconid was the fourth cusp to be initiated, it was the last to coalesce. In the present paper Smith et al. look at three teeth, two (a dm_2 and an M_1) from the jaw of one individual and the third (an M_1) from the jaw of a second individual. They found that the differences in the development of the dm_2 and the M_1s were greater than the differences in the development of the two M_1s. The title of their paper suggests that the authors have generated a "computer model of dental development". It would have been more accurate to say the authors have presented a method that uses computers to help reconstruct the ontogeny of the enamel cap.

Comparative studies of primate growth and development have come a long way since 1924, and a fair distance since 1996. This volume captures a snapshot of what we must hope will be an ongoing, dare I say developmental, process.

References

Avishai, G., Muller, R., Gabet, Y., Bab, I., Zilberman, U., Smith, P., 2004. New approach to quantifying developmental variation in the dentition using serial microtomographic imaging. Microscopy Research and Techniques 65, 263–269.

Butler, P.M., 1939. Studies of the mammalian dentition – differentiation of the postcanine dentition. Proceedings of the Zoological Society of London Series B 109, 1–36.

Braga, J., Heuze, Y., 2007. Quantifying variation in human dental development sequences: An EVO-DEVO perspective. In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht. pp. 231–235.

Dahlberg, A.A., 1945. The changing dentition of Man. Journal of the American Dental Association 32, 676–690.

Dean, M.C., 1995. The nature and periodicity of incremental lines in primate dentine and their relationship to periradicular bands in OH 16 (*Homo habilis*): In: Moggi-Cecchi, J. (Ed.), Aspects of Dental Biology: Palaeontology, Anthropology and Evolution. International Institute for the Study of Man, Florence, pp. 239–265.

Dean, M.C., Beynon, A.D., Thackeray, J.F., Macho, G.A., 1993. Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. American Journal of Physical Anthropology 91, 401–419.

Dean, M.C., Scandrett, A.E., 1996. The relation between long-period incremental markings in dentine and daily cross-striations in enamel in human teeth. Archives of Oral Biology 41, 233–241.

Demirjian, A., Goldstein, H., Tanner, J.M., 1973. A new system of dental age assessment. Human Biology 45, 211–227.

Hlusko, L.J., Mahaney, M.C., 2007. Of mice and monkeys: quantitative genetic analyses of size variation along the dental arcade. In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht. pp. 231–235.

Kangas, A.T., Evans, A.R., Thesleff, I., Jernvall, J., 2004. Nonindependence of mammalian dental characters. Nature 432, 211–214.

Lucas, P., 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge.

Moorrees, C.F.A., Fanning, E.A., Hunt, E.E., 1963. Age variation of formation stages for ten permanent teeth. Journal of Dental Research 42, 1490–1502.

Monge, J., Mann, A., Stout, A., Roger, J., Wadenya, R., 2007. Dental calcification stages of the permanent M1 and M2 in U.S. children of African American and European American ancestry born in the 1990s. In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht. pp. 231–235.

Schroeder, H.E., 1991. *Oral Structural Biology.* Georg Thieme Verlag, Stuttgart.

Schultz, A.H., 1924. Growth studies on primates bearing upon Man's evolution. American Journal of Physical Anthropology 7, 149–164.

Schwartz, G.T., 2005. Developmental processes and canine dimorphism in primate evolution. Journal of Human Evolution 48, 97–103.

Schwartz, G.T., Godfrey, L.R., Mahoney, P., 2007. Inferring primate growth, development and life history from dental microstructure: the case of the extinct Malagasy lemur, *Megaladapis.* In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht. pp. 231–235.

Shellis, R.P., 1984. Variations in growth of the enamel crown in human teeth and a possible relationship between growth and enamel structure. Archives of Oral Biology 29, 697–705.

Shellis, R.P., 1998. Utilization of periodic markings in enamel to obtain information on tooth growth. Journal of Human Evolution 35, 387–400.

Skinner, M.M., Kapadia, R., 2005. An evaluation of microCT for assessing the 3D concordance of dental trait expression between the dentin-enamel junction and the outer enamel surface of modern human molars. American Journal of Physical Anthropology Supplement 40, 191–192.

Smith, P., Müller, R., Gabet, Y., Avishai, G., 2007. A computerized model for reconstruction of dental ontogeny: a new tool for studying evolutionary trends in the dentition. In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht. pp. 231–235.

Spoor, F., Zonneveld, F., 1998. Comparative review of the human bony labyrinth. Yearbook of Physical Anthropology 41, 211–251.

Wood, B.A., 1996. Hominin paleobiology – have studies of comparative development come of age? American Journal of Physical Anthropology 99, 9–15.

Wood, B.A., Stack, C.G., 1980. Does allometry explain the differences between "gracile" and "robust" australopithecines? American Journal of Physical Anthropology 52, 55–62.

Zihlman, A., Bolter, D., Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. Proceedings of the National Academy of Sciences of the USA 101, 10541–10543.