NEWS

# Developmental Variation of the Primate Dentition: The 2011 AAPA Symposium in Honor of Don Reid

On April 15th, 2011, a special AAPA symposium was held in Minneapolis, Minnesota to celebrate Don Reid's influential contributions to the field of dental histology. Twenty presenters gathered to showcase state-of-the-art research on dental development and structure, share treasured stories, and express their gratitude for their recently retired colleague (Fig. 1). We begin this review with a brief history of Don's remarkable 50-year career, followed by a summary of the research presented in Minneapolis.

In 1961, at the age of 16, Don took a position as a histology technician in the Anatomy Department of Kings College (United Kingdom). His early work with Howard Tonge at the Dental School included assisting in groundbreaking research on calorie and protein deficiency effects in developing pig dentitions.[1–3] During this time, Don also began working with David Beynon at Newcastle University to investigate enamel mineralization.[4,5] In the early 1980s, along with David Beynon, Alan Boyde, Timothy Bromage, Chris Dean, Lawrence Martin, Peter Shellis, and Bernard Wood, Don's careful histological labors helped to usher in a revolutionary new approach to understanding the evolution of human growth and development.[6] Don, David, and Chris also began to document incremental dental development in living great apes and humans,[7–9] as well as in the Miocene hominoid genus *Proconsul*.[10] Until quite recently, these studies represented the only available comparative histological data, illuminating important aspects of hominoid life history and systematics. In 2000, Newcastle University awarded Don a Ph.D. for his prolific research on primate dental development, followed by a 2003 appointment as a Lecturer in recognition of his invaluable role at the Dental School.

Perhaps Dr. Reid's most significant contribution, in addition to his patient mentorship and collaboration with dozens of scholars, has been his seminal research on developmental variation in modern humans. Thousands of hours of histological preparation and analysis have demonstrated that modern human populations do not all develop their teeth identically,[11,12] facilitating more precise comparisons with fossil hominins and nonhuman primates.[13–16] Studies of modern human dental development have also established that external tooth crown increments (perikymata) are not laid down at a uniform rate from the beginning to end of crown formation.[11,17] These results have redefined the aging of linear enamel hypoplasias and serial isotopic samples of tooth crowns, calling into question previous bioarcheological and isotopic studies that assumed spatial and temporal equivalence. Moreover, Reid and Ferrell[18] demonstrated a novel inverse relationship between the number of long-period growth lines (perikymata, Retzius lines) and their intrinsic temporal periodicity. This relationship has helped to contextualize the marked degree of variation in long-period line numbers in human populations and has had important implications for studies of fossil hominins.[13]

A survey of research presented during the 2011 symposium underscores how the field continues to evolve, due in part to Don's important contributions, and the growing connections among dental histologists. All 20 participants are linked with Dr. Reid by no more than three degrees of academic separation; in this field nearly everyone is a collaborator, mentee, or one of Don's "grand-students" (Fig. 2). Presentations focused on dental studies of fossil primates, living nonhuman primates, and modern humans.

Papers on fossil dental development ranged from the Eocene adapid *Leptadapis magnus* to *Homo neanderthalensis*, often emphasizing relationships among dental development, life history, diet, and systematics.

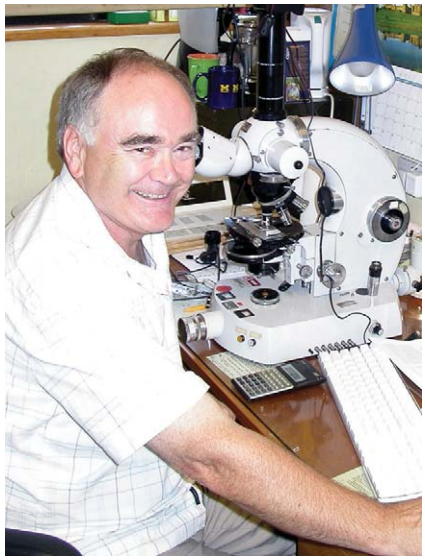

Figure 1. Don Reid at work with his beloved microscope. Photo courtesy of Wendy Dirks. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

Wendy Dirks (Newcastle) and colleagues showed that *Leptadapis magnus*, which had morphological crown features indicative of folivory, also had characteristics of rapid molar development associated with folivory. Plio-Pleistocene hominins were represented by two papers. Rodrigo Lacruz (University of Southern California) and colleagues reported differences in cusp and crown base areas between *Australopithecus anamensis* and *Australopithecus afarensis* molars, adding additional morphological weight to taxonomic distinctions. Paul Tafforeau and co-workers, represented by coauthor Joane Pouech (European Synchrotron Radiation Facility, Grenoble) presented synchrotron imaging data from juvenile *Paranthropus robustus* and *Homo* sp. dentitions from Drimolen, South Africa (2.0-1.5 mya). Short formation times were found in *Paranthropus* molar cusps as compared to *Homo*, underscoring developmental differences between these two coexisting genera. Tanya Smith (Har-

Figure 2. Participants at the AAPA 2011 symposium in honor of Don Reid. From left to right: Charuwan Manmee, Halszka Glowacka, Akiko Kato, Joane Pouech, Robin Feeney, Jacopo Moggi-Cecchi, Kierstin Catlett, Laurie Godfrey, Russell Hogg, Debbie Guatelli-Steinberg, Julia Boughner, Rodrigo Lacruz, Sarah Martin, Sarah Holt, Bernard Wood, Daniel Antoine, Wendy Dirks, Don Reid, Simon Hillson, Justyna Miszkiewicz, Daniel Green, Patrick Mahoney, Tanya Smith and Gary Schwartz. Photo courtesy of Brett Nachman and Daniel Green. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

vard) and colleagues discussed recent work on ontogenetic differences between Neanderthals and modern humans. By also using synchrotron virtual histology, they demonstrated that Neanderthals had shorter periods of dental development than modern humans, suggesting that Neanderthals may also have had more rapid life histories than modern humans.

Across the primate order, the pace of primate life histories is strongly correlated with the timing of dental development, brain size, and body size.[19] Gary Schwartz and Jay Kelley (ASU) summarized current perspectives on the relationships between age at molar eruption and other life history-related variables, suggesting that early hominins erupted their first molars at surprisingly young ages relative to wild apes. Daniel Green (Harvard) and colleagues demonstrated that great apes show broadly similar rates of enamel secretion and periods of crown formation, despite differences in crown size. Notably, large gorilla molar teeth form through rapid recruitment of enamel-forming cells, which may relate to their accelerated life histories.

The nature of relationships among dental development, somatic development, skeletal development, and life history is complex. Indeed, Kierstin Catlett (ASU) and colleagues showed that within the Indriid-Palaeopropithecid clade, the timing of dental development is not related to species-level differences in brain and body size, and it is rapid relative to somatic and cranial growth. Factors such as diet and local ecology may be critical for understanding variation. Russell Hogg (Univ. Missouri) and colleagues presented complementary research demonstrating differences between haplorrhines and strepsirrhines in the relationships among long-period line periodicities and life history-related variables (body mass, brain mass, and metabolic rate). The decoupling of dental and somatic growth has been known from the modern human literature for some time.[20] Julia Boughner's (Univ. Saskatchewan) paper provided an exciting glimpse into the molecular mechanisms that may underlie this independence. She contrasted gene expression in embryonic mouse mandibles from a normal strain with those from a "toothless" strain in which mandibular development proceeds normally but tooth development is arrested before the bud stage. In these mice, genes known to be involved in mandibular morphogenesis were expressed at normal levels, while most genes with known involvement in dental development were not.

In his highly anticipated comments, Dr. Reid called for additional research on variation in modern human dental development. Several symposium papers strived toward this goal. Fernando Ramirez-Rozzi (CNRS) and Marta Lahr (paper presented by Rodrigo Lacruz) studied dental growth in Australian aborigines, reporting crown formation periods at the long end of the known modern human range. Patrick Mahoney (Kent) and colleagues compared dental development in Fulbe pastoralists and Nso agriculturalists from Cameroon. While the diets of these populations differ significantly, which was supported by isotopic work, enamel development does not appear to differ.

Daniel Antoine (British Museum) and colleagues added to the limited histological record on crown initiation timing by examining post-Medieval children of known age. Until recently, data on modern human crown initiation ages have been derived from radiographic studies, which cannot detect the earliest stages of mineralization.[5] Interestingly, Antoine and colleagues documented earlier anterior tooth initiation ages in this sample than have been found in Europeans.[9] Sarah Holt (Ohio State) presented novel findings on enamel secretion rates in deciduous teeth from a contemporary Italian

population and a Roman archeological site, which did not appear to differ between populations.

Debbie Guatelli-Steinberg and coworkers investigated the relationship between enamel extension rates, the rate at which enamel-forming cells differentiate along the enamel-dentine junction, and the distribution of perikymata on the lateral enamel surface of modern human teeth. They found a decline in the rate of extension that corresponds to a decrease in perikymata spacing. The study was motivated by the fact that different hominin species exhibit variation in perikymata distribution.[21,22]

While the preceding studies focused on normal tooth development, several papers addressed disrupted growth. Simon Hillson (UCL) and Daniel Antoine presented a carefully illustrated case study of enamel hypoplasia in an enigmatic post-Medieval individual. They documented a range of synchronous developmental defect manifestations that differed within teeth and would not have been evident from tooth surfaces alone. Justyna Miszkiewicz (Kent) and Patrick Mahoney found a relationship between linear enamel hypoplasia (formed during childhood) and adult age at death in Medieval burials from Canterbury, UK. Higher status individuals had lower frequencies of enamel hypoplasias and later ages at death than did lower status individuals. Sarah Martin (Ohio State) and colleagues examined the relationships between crown formation time, fluctuating asymmetry, and developmental defects (linear enamel hypoplasias) in the canines of male and female gorillas and gibbons. They found that male gorilla canines, which grow over a longer period than females (or gibbons of either sex), show the highest degree of developmental disturbance, while monomorphic gibbons do not show sex differences.

The symposium also included cutting-edge research on modern human dental tissue structure and chemistry. Robin Feeney (Univ. Dublin) and colleagues reported differences in dental tissue proportions between male and female modern human molars. Males were found to have larger dentine and pulp volumes and enamel-dentine junction areas than do females, leading to relatively lower average and relative enamel thickness. Charuwan Manmee (Newcastle) and colleagues presented a histologically informed assessment of lead levels in children from northern England. They found that lead levels occur at the same age when sampled along several transects in the circumpulpal dentine, suggesting that only one transect is required to assess age-specific lead exposure in dentine.

The closing discussion was led by Bernard Wood (George Washington University), who related tales of working with David Beynon and acknowledging the critical "behind-the-scenes" role Don played in early studies of fossil hominin and living primate development. Bernard also highlighted something Don's colleagues and students know well: his openness and patience with the rest of us novice histologists is unparalleled. Beyond the significant scientific contributions he has made to the study of dental development, Don Reid's unflagging spirit of generosity and collegiality is an inspirational lesson for all evolutionary anthropologists.

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