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Preface

Dental tissue studies: 2D and 3D insights into human evolution

Students of human and primate evolution cannot escape the reality that much of what we know about evolution derives from dental remains, which are "taphonomically robust" relative to the other hard and soft tissues constituting mammalian forms. Paleoanthropologists have labored for over a century to assess aspects of tooth size, shape, and number in order to understand evolutionary changes and relationships in the primate lineage. In some instances, teeth represent the sole evidence of extinct primate species (e.g., *Chinjipithecus atavus*; von Koenigswald, 1981), while in many other cases, dental remains make up the vast majority of fossil evidence documenting a species (e.g., *Gigantopithecus blacki*, reviewed in Kupczik and Dean, 2008). Recent molecular and developmental studies have issued cautionary conclusions regarding traditional analyses of dental remains (e.g., Collard and Wood, 2000; Hlusko et al., 2004; Kangas et al., 2004). While analyses of tooth size and shape remain relevant for addressing particular questions, it is clear that new approaches to interpreting primate dental tissues are needed. This special issue of *Journal of Human Evolution* features contributions focused on assessing aspects of dental development and structure using two- and three-dimensional (2D and 3D) approaches, ranging from dental histology to phase contrast X-ray synchrotron microtomography. The contributions to the special issue are intended to synthesize and advance previous 2D and 3D dental tissue research with newly developed analytical approaches and expanded comparative information on internal and external aspects of primate tooth growth and form.

On September 20–23, 2006, the Department of Human Evolution at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) and the European Virtual Anthropology Network (EVAN) co-hosted an international Dental Tissues Workshop at the MPI-EVA in Leipzig, Germany. This event provided a key training opportunity for EVAN fellows, as well as a chance for leading specialists to discuss and debate how dental tissue research is advancing the study of human evolution. Research reports, keynote lectures, and interactive workshops on theoretical and technical aspects of dental tissue research were presented, and thirty-six individuals from ten countries took part (Fig. 1). Keynote lectures on virtual paleoanthropology, life-history variation, and dentine development were delivered by Jean-Jacques Hublin, B. Holly Smith, and M. Christopher Dean, respectively. Workshops held in state-of-the-art laboratories demonstrated the acquisition and analysis of micro-focal computed tomographic (μCT) data, as well as the preparation of histological sections and quantification of incremental dental development. Original research reports were presented within the themes of "New Dimensions and Research Innovations," "Primate Evolution," and "Hominin Evolution." A number of these reports are featured in the pages of this volume, which may be divided into 2D and 3D studies of dental microstructure and tooth growth (Dean and Vesey, 2008; Guatelli-Steinberg and Reid, 2008; Reid et al., 2008; Smith, 2008; Tafforeau and Smith, 2008; Zhao et al., 2008) and 3D studies of tooth structure (Kupczik and Dean, 2008; Olejniczak et al., 2008; Skinner et al., 2008).

The Leipzig Dental Tissues Workshop also marked the 10-year anniversary of the international workshop on Enamel Structure and Development, and its Application in Hominid Evolution and Taxonomy" held in Paris, France, in 1996 (see Ramirez Rozzi, 1998), and the 17-year anniversary of the "Primate Dental Symposium" held at the 1989 American Association of Physical Anthropology Meetings in San Diego, California (see Winkler and Swindler, 1991). Studies of incremental tooth growth have continued to increase in number since the early 1980s (Fig. 2). During the past two decades, *Journal of Human Evolution*, in particular, has served as an important forum for the dissemination of ideas and data on hominoid incremental tooth development, representing the single largest publisher of this research (more than 20% of the 95 papers in Fig. 2).

The research reports delivered in Leipzig demonstrate that the study of dental tissues has progressed over the past few decades. For example, debates about the fundamental nature of incremental features have been resolved (reviewed in FitzGerald, 1998; Smith, 2006), as have issues of life-history differences between early hominins and modern humans (reviewed in Winkler and Swindler, 1991; Smith and Tompkins, 1995). The potential for incremental features to provide evidence for fossil ape and human life history continues to be demonstrated in a growing number of fossil taxa (e.g., Dean et al., 2001; Kelley and Smith, 2003; Dean, 2006; Smith et al., 2007a; Zhao et al., 2008). In addition, studies of incremental development are now regularly incorporating sample sizes suitable for statistical analyses (e.g., Schwartz et al., 2001; Smith et al., 2007b,c; Guatelli-Steinberg and Reid, 2008; Reid et al., 2008), facilitating the transition

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Fig. 1. Participants in the Dental Tissues Workshop held at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Front row (left to right): Holly Smith, Tanya Smith, Jean-Jacques Hublin, Yi Seung-Won, Sam Cobb, Don Reid, Paul Tafforeau, Matt Skinner, Pam Walton. Second row (left to right): Wendy Dirks, David Keinan, Luca Fiorenza, Mandy Teichmann, Almudena Estalrrich, Fernando Ramirez Rozzi, Ottmar Kullmer, Mark Skinner, Lingxia Zhao, Chia Lin Lo. Third row (left to right): Fred Spoor, Gal Avishai, Flora Gröning, Priscilla Bayle, Philipp Gunz, Heiko Temming, Samuel García Vargas, Olga Panagiotopoulou, Anthony Olejniczak, Jay Kelley, Kornelius Kupczik, Robin Feeney, and Chris Dean. (Missing from photo: Kierstin Catlett, Bill Kimbel, Thomas Koppe, Ralf Radlanski.)

from descriptive studies to an analytical, comparative biological approach.

Advances have also been made in the assessment of modern human population variation; histologically derived crown-formation data for each tooth type are now available for populations from northern England and southern Africa (Reid and Dean, 2000; Reid and Dean, 2006; Reid et al., 2008) and for multiple dentitions of chimpanzees and gorillas (Beynon et al., 1991; Reid et al., 1998; Schwartz et al., 2006; Smith et al., 2007b). Dentine development and root growth data are increasing for a number of living and fossil apes and humans (reviewed in Dean, 2006, 2007; Smith, 2008; see also Dean and Vesey, 2008).

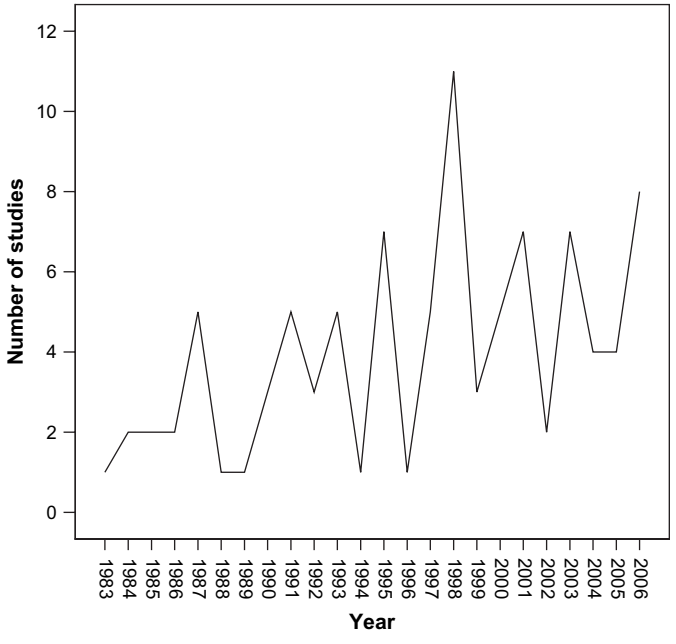

Fig. 2. Number of studies of incremental development in hominoid primates from 1983 to 2006 (data from Table 1 of Smith, 2008). More than 10% of these papers appeared in special issues of *American Journal of Physical Anthropology* (Volume 86, Number 2, 1991) and *Journal of Human Evolution* (Volume 35, Number 4/5, 1998), resulting from the San Diego Symposium and the Paris Workshop. Following 1998, there has been an average of five studies published per year.

Nondestructive approaches to characterizing tooth growth continue to be developed, including portable confocal microscopy (Bromage et al., 2007), and the use of μCT for the assessment of cuspal enamel thickness (Smith et al., 2006, 2007a). One promising avenue for future developmental studies is the application of phase contrast X-ray synchrotron microtomography (Tafforeau, 2004; Tafforeau et al., 2006, 2007; Tafforeau and Smith, 2008), which facilitates nondestructive assessments of internal features, crown formation time, and age at death in fossil hominin dentitions (e.g., Smith et al., 2007a).

Studies of enamel thickness and internal structure have also recently benefited from rapid advances in nondestructive μCT; the development and availability of μCT has led to a number of recent Ph.D. dissertations on tooth structure (e.g., Kupczik, 2003; Tafforeau, 2004; Olejniczak, 2006). Dental tissue volumes (e.g., Avishai et al., 2004; Kono, 2004; Macchiarelli et al., 2006; Smith et al., 2006; Olejniczak et al., 2008) and the morphology of the enamel-dentine junction (e.g., Olejniczak et al., 2004, 2007a; Skinner et al., 2008) may now be quantified nondestructively and accurately (Tafforeau, 2004; Olejniczak and Grine, 2006). Visualization of previously inaccessible aspects of dental anatomy facilitates refined assessments of

primate diets and characters employed in cladistic and taxonomic analyses (e.g., Brunet et al., 2005; Kupczik and Dean, 2008; Olejniczak et al., 2008; Skinner et al., 2008).

The application of synchrotron microtomography in paleoanthropology, which represents a complementary approach to laboratory μCT (Olejniczak et al., 2007b), remains a promising avenue for future research, facilitating the integration of developmental and structural studies (Tafforeau, 2004; Smith et al., 2006; Tafforeau et al., 2006; Smith et al., 2007a). As noted by Olejniczak et al. (2008), dental tissue research that centers on the elucidation of the dental ''character complex'' (tissue development, thickness, shape, and volume) is emerging with these new technological advancements as a powerful analytical approach to interpret the human and primate fossil record. We hope that this volume serves to highlight some of these cutting-edge applications, and provides a perspective on the future of paleoanthropological dental-tissue research.

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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. Microsc. Res. Tech. 65, 263–269.

Beynon, A.D., Dean, M.C., Reid, D.J., 1991. Histological study on the chronology of the developing dentition in gorilla and orangutan. Am. J. Phys. Anthropol. 86, 189–203.

Bromage, T.G., Lacruz, R., Perez-Ochoa, A., Boyde, A., 2007. Portable confocal scanning optical microscopy of *Australopithecus africanus* enamel structure. In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht, pp. 193–209.

Brunet, M., Guy, F., Pilbeam, D., Lieberman, D.E., Likius, A., Mackaye, H.T., Ponce de León, M.S., Zollikofer, C.P.E., Vignaud, P., 2005. New material of the earliest hominid from the upper Miocene of Chad. Nature 434, 752–755.

Collard, M., Wood, B., 2000. How reliable are human phylogenetic hypotheses? Proc. Natl. Acad. Sci. U.S.A. 97, 5003–5006.

Dean, M.C., 2006. Tooth microstructure tracks the pace of human life-history evolution. Proc. R. Soc. B 273, 2799–2808.

Dean, M.C., 2007. A radiographic and histological study of modern human lower first permanent molar root growth during the supraosseous eruptive phase. J. Hum. Evol. 53 (6), 635–646.

Dean, C., Leakey, M.G., Reid, D., Schrenk, F., Schwartz, G.T., Stringer, C., Walker, A., 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414, 628–631.

Dean, M.C., Vesey, P., 2008. Preliminary observations on increasing root length during the eruptive phase of tooth development in modern humans and great apes. J. Hum. Evol. 54, 258–271.

FitzGerald, C.M., 1998. Do enamel microstructures have regular time dependency? Conclusions from the literature and a large-scale study. J. Hum. Evol. 35, 371–386.

Guatelli-Steinberg, D., Reid, D.J., 2008. What molars contribute to an emerging understanding of lateral enamel formation in Neandertals vs. modern humans. J. Hum. Evol. 54, 236–250.

Hlusko, L.J., Suwa, G., Kono, R.T., Mahaney, M.C., 2004. Genetics and the evolution of primate enamel thickness: a baboon model. Am. J. Phys. Anthropol. 124, 223–233.

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

Kelley, J., Smith, T.M., 2003. Age at first molar emergence in early Miocene *Afropithecus turkanensis* and life-history evolution in the Hominoidea. J. Hum. Evol. 44, 307–329.

Kono, R., 2004. Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. Anthropol. Sci. 112, 121–146.

Kupczik, K., 2003. Tooth root morphology in primates and carnivores. Ph.D. Dissertation, University College London.

Kupczik, K., Dean, M.C., 2008. Comparative observations on the tooth root morphology of *Gigantopithecus blacki*. J. Hum. Evol. 54, 196–204.

Macchiarelli, R., Bondioli, L., Debénath, A., Mazurier, A., Tournepiche, J.-F., Birch, W., Dean, C., 2006. How Neanderthal molar teeth grew. Nature 444, 748–751.

Olejniczak, A.J., 2006. Micro-computed tomography of primate molars. Ph.D. Dissertation, Stony Brook University.

Olejniczak, A.J., Gilbert, C.C., Martin, L.B., Smith, T.M., Ulhaas, L., Grine, F.E., 2007. Morphology of the enamel-dentine junction in sections of anthropoid primate maxillary molars. J. Hum. Evol. 53, 292–301.

Olejniczak, A.J., Grine, F.E., 2006. Assessment of the accuracy of dental enamel thickness measurements using micro-focal X-ray computed tomography. Anat. Rec. 288A, 263–275.

Olejniczak, A.J., Martin, L.B., Ulhaas, L., 2004. Quantification of dentine shape in anthropoid primates. Ann. Anat. 186, 479–485.

Olejniczak, A.J., Tafforeau, P., Feeney, R.N.M., Martin, L.B., 2008. Three-dimensional primate molar enamel thickness. J. Hum. Evol. 54, 187–195.

Olejniczak, A.J., Tafforeau, P., Smith, T.M., Temming, H., Hublin, J.-J., 2007. Compatibility of microtomographic imaging systems for dental measurements. Am. J. Phys. Anthropol. 134, 130–134.

Ramirez Rozzi, F.V., 1998. Enamel structure and development and its application in hominid evolution and taxonomy. J. Hum. Evol. 35, 327–330.

Reid, D.J., Dean, M.C., 2000. The timing of linear hypoplasias on human anterior teeth. Am. J. Phys. Anthropol. 113, 135–139.

Reid, D.J., Dean, M.C., 2006. Variation in modern human enamel formation times. J. Hum. Evol. 50, 329–346.

Reid, D.J., Guatelli-Steinberg, D., Walton, P., 2008. Variation in modern human premolar enamel formation times: Implications for Neandertals. J. Hum. Evol. 54, 225–235.

Reid, D.J., Schwartz, G.T., Dean, C., Chandrasekera, M.S., 1998. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. J. Hum. Evol. 35, 427–448.

Schwartz, G.T., Reid, D.J., Dean, C., 2001. Developmental aspects of sexual dimorphism in hominoid canines. Int. J. Primatol. 22, 837–860.

Schwartz, G.T., Reid, D.J., Dean, M.C., Zihlman, A.L., 2006. A faithful record of stressful life events preserved in the dental developmental record of a juvenile gorilla. Int. J. Primatol. 22, 837–860.

Skinner, M.M., Wood, B., Boesch, C., Olejniczak, A.J., Rosas, A., Smith, T.M., Hublin, J.-J., 2008. Dental trait expression at the enamel-dentine junction of lower molars in extant and fossil hominoids. J. Hum. Evol. 54, 173–186.

Smith, B.H., Tompkins, R.L., 1995. Toward a life history of the Hominidae. Annu. Rev. Anthropol. 24, 257–279.

Smith, T.M., 2006. Experimental determination of the periodicity of incremental features in enamel. J. Anat. 208, 99–113.

Smith, T.M., 2008. Incremental dental development: methods and applications in hominoid evolutionary studies. J. Hum. Evol. 54, 205–224.

Smith, T.M., Olejniczak, A.J., Tafforeau, P., Reid, D.J., Grine, F.E., Hublin, J.-J., 2006. Molar crown thickness, volume, and development in South African Middle Stone Age humans. S. Afr. J. Sci. 102, 513–517.

Smith, T.M., Tafforeau, P.T., Reid, D.J., Grün, R., Eggins, S., Boutakiout, M., Hublin, J.-J., 2007a. Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc. Natl. Acad. Sci. U.S.A. 104, 6128–6133.

Smith, T.M., Reid, D.J., Dean, M.C., Olejniczak, A.J., Martin, L.B., 2007b. Molar development in common chimpanzees (*Pan troglodytes*). J. Hum. Evol. 52, 201–216.

Smith, T.M., Reid, D.J., Dean, M.C., Olejniczak, A.J., Ferrell, R.J., Martin, L.B., 2007c. New perspectives on chimpanzee and human dental development. In: Bailey, S.E., Hublin, J.-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht, pp. 177–192.

Tafforeau, P., 2004. Phylogenetic and functional aspects of tooth enamel microstructure and three-dimensional structure of modern and fossil primate molars: contributions of X-ray synchrotron microtomography. Ph.D. Thesis, Université de Montpellier II.

Tafforeau, P., Bentaleb, I., Jaeger, J.-J., Martin, C., 2007. Nature of laminations and mineralization in rhinoceros enamel using histology and X-ray synchrotron microtomography: potential implications for palaeoenvironmental isotopic studies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 246, 206–227.

Tafforeau, P., Boistel, R., Boller, E., Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P., Feist, M., Hoszowska, J., Jaeger, J.-J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A., Nemoz, C., Thibault, X., Vignaud, P., Zabler, S., 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. Appl. Phys. A 83, 195–202.

Tafforeau, P., Smith, T.M., 2008. Nondestructive imaging of hominoid dental microstructure using phase contrast X-ray synchrotron microtomography. J. Hum. Evol. 54, 272–278.

Winkler, L.A., Swindler, D.R., 1991. Primate dental symposium: old and new questions, new trends. Am. J. Phys. Anthropol. 86, 107–111.

von Koenigswald, G.H.R., 1981. A possible ancestral form of *Gigantopithecus* (Mammalia, Hominoidea) from the Chinji Layers of Pakistan. J. Hum. Evol. 10, 511–515.

Zhao, L., Lu, Q., Zhang, W., 2008. Age at first molar emergence of *Lufengpithecus lufengensis* and its implications for life-history evolution. J. Hum. Evol. 54, 251–257.

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