Dental Perspectives on Human Evolution

Vertebrate Paleobiology and Paleoanthropology

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Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology

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When faced with choosing a topic to be the focus of the first symposium in Human Evolution at the Max Planck Institute for Evolutionary Anthropology in Leipzig, a paleoanthropological perspective of dental anthropology was a natural choice. Teeth make up a disproportionate number of the fossils discovered. They represent strongly mineralized organs of compact shape, which allow better preservation in geological deposits and archaeological sites than any other part of the skeleton. As a result, since the discoveries of the first fossils of extinct species, vertebrate paleontology has been built primarily on analyses of teeth. The first dinosaur identified in 1825 by Gideon Mantell was actually a dinosaur tooth. Paleoanthropology is no exception to this rule, as teeth represent, by far, the most abundant material documenting different species of extinct non-human primates and hominins. As such, much of what we know about non-human primate and hominin evolution is based on teeth.

Teeth have been a focus of interest for physical anthropologists over many generations. Teeth provide a multitude of information about humans – including cultural treatment, pathology, morphological variation, and development. The presence of culturally induced wear (toothpick grooves, for example) reveals something about what humans were doing with their teeth in the past. Pathologies, such as enamel hypoplasia and dental caries, are informative for understanding the health and nutritional status of individuals and populations. Dental morphological variation among living humans has proven to be important for assessing biological relationships among recent groups. Finally, the dental sequence of calcification and eruption patterns remain, even today, the easiest way to assess the individual age of nonadult modern humans. Although dental anthropology has a long history in physical anthropology, the recent years have brought a number of new discoveries, new methods, and a renewal of interest in using the teeth to answer questions about human and nonhuman primate evolution. The goals of studies focusing on fossil humans are similar to those of recent humans noted above. In addition, of particular interest are the biological relationships among extinct species, the amount of variation one should expect in fossil species, and the polarity of dental characters.

To date, the developmental pathways of most of the skeletal features routinely used in paleoanthropological studies remain obscure. We know that the genotype interacts with the environment in a complex manner. This interaction produces a pattern that we attempt to interpret in phylogenetic and taxonomic ways, but from which we also attempt to extract other biological information. Unfortunately, the level of integration among skeletal (primarily cranial) features that are most often considered independent is, in many cases, still to be explored. Tooth size and, even more, morphology are under strong genetic control. Because dental germs are formed in an early stage of individual development while the individual is still in utero, teeth may represent organs that are widely independent from environmental influences. While sometimes considered 'less exciting' than, say, skulls, the most abundant fossils might, in fact, be some of the most meaningful for paleontological studies. In recent years, the development of 3D morphometrics and the systematic coding of non-metric traits of the dentition have opened new avenues for the assessment of dental morphological variation, which supersedes the earlier, rather disappointing, results based on simple linear measurements of length and breadth.

Another special feature of the dentition is that, in contrast to the rest of the skeleton, it is not subject to major remodeling during the course of an individual's life (aside from attrition). Enamel tissue is laid down in the early stages of life and becomes a mostly closed system interweaving mineralized prisms and organic matter. Teeth are not just an abundant fossil material that can be found in the field; they also represent fossilized stages of the life history of an individual. Because enamel is very hard and undergoes few exchanges with the surrounding environment, teeth preserve chemical signals that can be analyzed for the establishment of the geological age of specimens, as well as for the understanding of the individual biology at different ages of life. The explosive development of isotopic studies has made it possible to study dietary differences among individuals as well as environmental conditions at different stages of the life in ancient humans. In some cases, intriguing aspects of daily life, mating strategies, or landscape occupation of past populations have been revealed. It is also inside the teeth that we are more likely to find preserved fossil molecules such as proteins, which allow us to access fascinating aspects of the biology of our remote predecessors.

Soon after their eruption into the oral cavity, teeth represent a major interface between the individual and its environment, and their wear patterns and pathologies become another major source of information for both dietary and non-dietary behaviors. While the gross morphology of the tooth can tell us what an organism is capable of processing, it is the actual wear patterns on the enamel surface that tell us how this organism was actually using its teeth. Although not without problems, microwear analyses have provided a wealth of information on dietary differences in extant primates and humans. These have recently been supplemented by topographical models in three dimensions that allow angles, planes and valleys to be investigated and by three-dimensional analyses of wear planes. Both provide information on dental function and occlusion.

Once we move below gross tooth morphology a proverbial 'whole new world' opens up. New methods allow us to visualize the structures underlying tooth enamel as well as the microscopic intricacies of enamel itself. Recent research in this area has been extremely important to human paleontology, especially with regard to dental development and life history – two current and important issues in physical anthropology. The pace of development, brain maturation, length of learning period, reproductive patterns and longevity are crucial issues for understanding biological and social changes during the course of human evolution. Until recently this has been mostly a field of speculation based on the knowledge of extant apes and humans. The development of microstructural studies has revealed that dental tissues represent, by far, one of the best records of the conditions of the growth and development of individuals. The extent to which extinct hominin species are comparable to extant humans, or other large primates, has become a focus of interest for many studies. With the development of the use of new instruments such as the confocal microscope, micro-CT scanners, or the synchrotrons, researchers are now able to explore a new world inside our teeth.

One exciting aspect of publishing a volume on recent advances in dental paleoanthropological studies is the bringing together of multiple disciplines in which tooth morphology is currently being used to answer questions about human and non-human primate evolution. The different approaches mentioned here have been rapidly integrated as new methods to access biological information. Another is that here, perhaps to a greater extent than in other subfields of physical anthropology, an integration of the contributions coming from primatology and modern human variation is essential to develop meaningful interpretation of the fossil record. Dental anthropology has become a very multi-disciplinary field, by the scope of its studies as well as by the variety of techniques employed in recent analyses. In inviting the contributors of this volume to participate in its publication, we wanted to make available the state-of-the-art of our knowledge in this field. In addition, this project also illustrated the rapid progress in a variety of analytical methods that have recently emerged in the broader domain of biological anthropology.

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Introduction

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Teeth occupy a central place in the fossil evidence for human evolution. One reason for this lies in their complex biology. Strictly speaking, although teeth are preserved with the bones of the skeleton, they are biologically a separate entity; the dentition. Like bone, the three dental tissues, enamel, dentine and cement are calcium phosphate and organic composites and as the hardest parts of the body, bones and teeth are the part that remains in the fossil record, but the similarity ends there. Bone is a mineralized connective tissue, developing and remaining only within the body. It contains living cells, blood vessels and nerves. Enamel by contrast is a heavily mineralized epithelial tissue, visible on the surface of the body, containing no cells, blood or nervous supply. In effect, it is dead even in living creatures. Dentine only develops in contact with epithelium – part of the dermal armor in some ancient fish, but confined to the teeth in mammals. It also contains no complete cells, although processes from cells lining the pulp chamber inside the tooth pass through it, carried in the microscopic tubes that characterize dentine structure. Of the three dental tissues, cement is the most bone-like in composition. Both contain living cells, held in tiny chambers called lacunae, and the collagen of the organic component has a dominant role in both structures, but in primates cement has a very different organization, contains no blood supply and acts only as an attachment for the ligament that holds the tooth into its socket.

The principal difference is that dental tissues do not turn over. Bone is continually replaced throughout life by the activities of its cells, the osteoclasts and osteoblasts. The rate varies through the skeleton, but each cubic centimeter of a major long bone is probably replaced almost completely over 10 years or so. The form of a bone is actively maintained, in response to the forces acting on it. As these alter, through injury and disease, changes in posture and activity, or physiology, the overall shape of the bone is remodeled by tissue turnover. Once formed, dental tissues in primates do not do this. They therefore retain the structures put in place by their development. It is possible to see and count these in microscope preparations. In addition, teeth are formed in childhood in their final shape and size, so their morphology can be compared directly between juveniles and adults. They have an intricate form which, because it remains as originally developed, should be easier to understand in relation to the activities of the genes of development.

By contrast, bones grow in size and change in proportions through childhood, so direct comparisons cannot be made in the same way. Teeth also retain the marks left by tooth wear and disease – their main response is to line their pulp chamber with secondary dentine to maintain the covering of dental tissue over the soft tissue of the pulp. Cement is also deposited on the root throughout the life of the tooth, and there is some suggestion that it might be more rapid in heavily worn teeth but there is no close relationship. Bones respond to disease and injury by remodeling – bone is lost in some areas and deposited in others, so that the shape changes. Fractures are mended, inflammation heals and so on. The contrast between teeth and bone is clearest in the continuous eruption of teeth as a response to wear. The teeth are continually pushed into the mouth to make up for the tissue worn away, but the teeth themselves do not provide the mechanism for this. Instead, the supporting bone remodels around them so that the sockets, teeth and all, migrate up through the alveolar process. In heavy wear rate populations, the wear progresses down the root as the socket shortens and, eventually, only a tiny root fragment remains which becomes lose and is lost when it becomes too short. The teeth literally wear out with very little response from dental tissues to the changes of wear, whilst the bone responds by constant remodeling.

Teeth thus have very much their own biology. They are formed by an intricate series of processes that leave their mark in dental tissues and can be studied to give a very detailed account of development. They present a highly variable array of intricate forms. Consideration of the mammals as a whole suggests that these forms represent not only adaptation to the gathering and processing of different types of food, but also to aspects of behavior, including sexual behavior, grooming and so on. There appears to be a strong inherited component in the development of different tooth forms and, although it will probably take many years to understand how these forms are controlled, the fact that tooth formation is a single event – there is no tissue turnover – should simplify the problem in the end. Thus, there seems a real prospect of using tooth morphology to reconstruct the adaptive mechanisms involved in primate evolution. Not only this, but the teeth and jaws seem to have been a major focus of change in the evolution in the hominids. For example, one of the strongest trends in the genus *Homo* has been the reduction of tooth size, together with the prominence of the jaws in the structure of the skull.

In many anatomy texts, teeth are presented as part of the alimentary canal. They touch every particle of the food passing through the mouth and are marked by this passage. Their form is presumably an adaptation to the nature of the food, and the effect of a lifetime's food processing. They wear down but, as they spend only a small fraction of the animal's lifespan as unworn, pristine specimens, the important aspect of tooth form from a selective point of view must presumably be the worn form which it presents throughout most of its life. To put it crudely, teeth are "designed" by evolution to be worn. This means that adaptive mechanisms need to be considered in terms of not only the activities and forces producing wear, but also the developing shape of the worn tooth and the changing way in which the teeth fit together (their occlusion) to adapt to the effects of wear. This approach was first proposed in the classic paper of P.R. Begg (1954), who was interested in the heavily worn teeth of Australian aborigine people, and considered that many of the dental problems of modern urban people arose because their teeth were insufficiently worn to function in the way that they were "designed" to do.

One reason for the central place of teeth in studies of human evolution is thus their information potential (see Foreword). Even a single small tooth can sometimes yield more information than a large pile of bones. They do, however, have another important point in their favor. The tissues and forms of teeth are adapted to surviving a lifetime in the mouth, where they are subject to continuous physical and chemical attack. Teeth are very tough, durable structures. The same properties have ensured that they dominate the fossil record in mammals. Bones are less able to resist weathering. They are also more likely to have been crushed in the jaws of carnivores and scavengers because the skull is overlain by less meat. For these reasons, most vertebrate paleontology is about teeth, and primate paleontology is no exception.

All this makes the conference described in this volume a particularly important event. Dental anthropology is a small specialty within the study of human evolution. Many more studies concentrate on the skull, for example, even though complete finds of skulls are relatively speaking rather rare. The term *dental anthropology* probably has its origin in a symposium of the Society for Study of Human Biology at the Natural History Museum in London, published as an edited volume by Don Brothwell (1963). One of the developing field's distinguishing features is that it has always involved a wide range of researchers, coming from dental schools and departments of anthropology, archaeology, anatomy and biology. It therefore encompasses a variety of approaches and research questions arising from very different points of view. Some researchers may, in fact, primarily be interested in teeth from the point of view of developmental biology and find evolution an interesting application, while others see teeth as only one approach to answering their questions which focus on human evolution. This gathering of converging interests has met regularly together at various venues since 1963 and has continued to find new enthusiasts to add to its founders. It has been extraordinarily productive, perhaps because of the variation in approach. Many of its international representatives came together in 2005 for the conference on *Dental perspectives in human evolution: state of the art research in dental anthropology*, at the Max Planck Institute for Evolutionary Anthropology, in Leipzig and their papers are presented in this volume.

The papers focus on three main themes: dental morphology, dental development and methods for examining teeth. Dental morphology in this context deals with variation in the size and shape of teeth from the hominid fossil record. Living primate species to a large extent show distinctive differences in tooth form, but they also show variation within species, particularly between the sexes. It is not clear how sexually dimorphic extinct species of primates might be, and the surviving specimens in any case represent just a few glimpses at what is likely to have been a considerable range in variation. One way in which the question can be approached is by examining variation of dental features within and between species of living apes to provide a context in which variation between fossils can be interpreted, as shown in Pilbrow's chapter. A similar approach is to look for trends and variation in hominid dental morphology, within and between well defined fossil species, and assemblages which may contain a number of taxa (chapters by Bailey and Wood, and by Moggi-Cecchi and Boccone). Similarly, cladistic and phenetic analysis of dental morphology can be used to test the way in which the hominid fossil record is divided into species (chapters contributed by Martinón-Torres and colleagues and by Manni and colleagues, respectively).

The established approach to dental morphology is to classify different features of the tooth crown and roots according to a standard system. The best known is the Arizona State University dental anthropology system (ASUDAS), although this is better adapted to the study of modern *Homo sapiens* than it is either to living apes or fossil hominids (see Bailey and Wood). It is necessary to add to the system those features which show more variation between apes and between the hominins of the Pliocene. With the arrival of digital photography, it has become straightforward to take instead measurements of lengths, angles and areas of features on the tooth crown, using image analysis software. This makes it possible to assess the size and spacing of features, rather than simply to score their state of development. Another step forward has been in the measurement of enamel thickness. One of the crucial trends in hominid evolution is a change in the thickness of the enamel layer which forms the surface of the crown. In the past, this has been limited by the necessity of sectioning teeth, but recent advances in micro-computed tomography (below) have allowed non-destructive measurements to a fine resolution. This makes possible the construction of detailed three dimensional models of the enamel cap and its thickness, as discussed by Olejniczak and colleagues and also by Gantt and colleagues.

If tooth shape and size are to provide evidence for the place of different fossils in hominid evolution, then it is important to understand how different morphologies develop and the way in which different characteristics of form might be inherited. In essence, this is the question of "how to make a tooth". One approach is through experimental biology, using animals such as laboratory mice in which the actions of different genes in the developmental sequence can be investigated. Another possibility is to carry out genetic analysis of dental features in a group of individuals whose pedigree is known, as for example provided by a captive colony of baboons (Hlusko and Mahaney).

As described above, once they are erupted into the mouth, the form of the teeth is altered by wear and they are unable to respond by remodeling. Most fossil hominids show evidence of very rapid tooth wear so, until the most recent times, the teeth of all but the youngest aged individuals are heavily worn. Ungar reasons that it is the form that teeth take after wear that must be important for the adaptive mechanisms that have driven evolution. Each species has a characteristic pattern of changes with wear that defines it just as clearly as the unworn form of the teeth. It is therefore necessary to define new ways in which to describe and compare the worn surfaces, as shown by Ulhaas and colleagues. It seems logical to suggest that the pattern of wear shown on the teeth should also reflect the nature of the diet and the way in which the dentition is used to process food. If this can be assessed, then at least some of the adaptive mechanisms acting on the form of the teeth should become clearer. One established approach to this question is the microscopic study of wear, known as dental microwear. Teaford gives a concise history of microwear studies ending with the most recent measurement and analytical techniques. These have addressed a number of difficult practical and theoretical difficulties and Esteberanz and colleagues (Part IV, Chapter 6) demonstrate the use of these with a range of fossil and recent hominid and pongid specimens.

Development of the teeth has been an important theme in dental anthropology from the beginning, and a large number of the papers in this volume are concerned with the topic. Modern human children develop over a longer period than other primates, and this is seen in the dentition as well as the rest of the body. This long schedule is related to the development of cognition and the behaviors that, in effect, make us human so one of the important questions for research on human evolution is the point at which this pattern of growth appeared – which fossil forms is it associated with? The fossil record represents a relatively small number of individuals which may represent any part of a range of variation, so one of the important questions is to understand the extent to which the pattern of growth varies within one species. To investigate large numbers of children, it is necessary to use x-rays, even though there are problems in assessing the stages of growth achieved and relating these scores to the development seen by direct observation of growing teeth. Braga and Heuze discuss practical and theoretical problems with the assessment of dental x-rays, and the way in which they show patterns of development that can be used to help interpret the fossil record. Monge and colleagues describe a study of variation in development seen in a large collection of dental x-rays from modern urban children.

The bulk of the papers on dental development, however, are based on the histology of dental enamel. Enamel's heavily mineralized structure enables it to survive well in fossils, with all its microscopic features intact. Amongst these features is a pattern of layering that reflects a circadian rhythm to the secretion of the enamel matrix during development. These so-called prism cross striations can provide a daily clock beat to determine the timing of key features in the growth of the dentition. One problem with studying growth rate in fossil material is that, to estimate it, a measure of age at death is needed against which the stage of development reached by a particular specimen. All age at death estimations in children are in turn based upon the sequence of growth changes, so the researcher quickly gets into a circular argument. In addition, growth standards for recent modern humans and living primates cannot be applied to extinct hominids without making large assumptions that are difficult to test. The regularity of the enamel clock is, however, maintained throughout the formation of all the teeth in the dentition and does not appear to be affected by factors which otherwise disturb growth of the body, such as childhood infections or dietary deficiencies. It also appears to work in a similar way in all primates. So counts of cross striations are believed to provide an independent measure of age against which the rate and timing of growth can be set. Schwartz and colleagues have used this to examine the relationship between body size and timing of dental development in living and extinct primates. In a similar way, T. Smith and colleagues have compared variation in the timing of molar crown formation in chimpanzees and humans, and Ramirez-Rozzi and Lacruz have compared the development of the bonobo with that of the chimpanzee. One of the difficulties with investigating the layered structure of enamel with thin sections is the damaged this causes to specimens. Another option is to examine the surface of the crown, usually by scanning electron microscopy of high resolution casts. The surface has a pattern of coarser, but still regular lines known as perikymata. In any one individual, there is a constant number of cross striations between them, so they too represent a regular rhythm. Even if the individual's rhythm is not known, it is possible to use the constancy of the perikymata rhythm to investigate variation in the way in which a tooth crown is formed at different points in its height, as discussed by Guatelli-Steinberg and colleagues. Finally, another possibility is to combine the approaches of biochemical analysis and histology. As outlined by Humphrey and colleagues, laser ablation mass spectrometry can analyze strontium:calcium ratios in very small areas in a tooth section, allowing a comparison between different phases of development. As these ratios change with weaning, it is possible to recognize the timing of this important event in the life history of an individual.

One of the common themes through this volume is the development of new techniques. Notably, Bromage and colleagues have developed a portable confocal light microscope, designed to be packed up and carried around the world to different museums. The advantage of confocal microscopy is that it makes it possible to focus a small way under the surface of translucent specimens and provide in-focus images of structures at that depth. It is possible to focus into the undamaged enamel surface in this way, and naturally formed fracture surfaces can provide information on deeper internal structures without damaging important specimens. Gantt and colleagues, Olejniczak and colleagues, and P. Smith and colleagues, describe the use of micro-computed tomography for the non-destructive imaging of three-dimensional internal structures such as the enamel-dentine junction. Conventional computed tomography, as routinely used in hospitals, creates "slices" of 1 mm or so (some give somewhat finer resolutions) of the subject. Micro CT can reduce this to as little as 5 μm (one micrometer is one thousandth of a millimeter). This makes it possible to study a large number of specimens and allows the measurement of dental architecture and the thickness of the enamel cap in variety of ways that have never before been possible. Another new technology is the arrival of instruments that can provide high resolution scans of the three-dimensional form of surfaces, again without damaging the specimen. Some of these are based on direct mechanical contact with the specimen, others with laser depth measurement and still others are based on confocal microscopy in which a stack of images at different focal depths is used to build the three-dimensional model. The latter currently provides the highest resolution. These surface models have allowed Ungar to follow the changing form of the occlusal surface with tooth wear, and also resolve many of the problems in measuring the scratches and pits of tooth wear at a microscopic scale as shown by Teaford, and by Estebaranz and colleagues. Three-dimensional models of the surface make it possible to measure the texture of microscopic wear in a variety of new ways.

This volume can be compared with the papers of the first dental anthropology conference in 1958 (Brothwell, 1963) and the "30 years on" symposium of the American Association of Physical Anthropologists in 1988 (Kelley and Larsen, 1991). It is only another 17 years since the latter, but the field has clearly moved a considerable way, not only in the techniques available and the knowledge base that has built up, but in the research questions that can now be asked.

References

Begg, P.R., 1954. Stone Age man's dentition. American Journal of Orthodontics 40, 298–383.

Brothwell, D.R., 1963. *Dental Anthropology*. Pergamon Press, London.

Kelley, M.A., Larsen, C.S., 1991. *Advances in Dental Anthropology*. Wiley-Liss, New York.

PART I

DENTAL EVOLUTION AND DENTAL MORPHOLOGY

1. Introduction

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The study of the external tooth morphology can be undertaken in a non-destructive and relatively inexpensive manner. All one needs are good eyes (or a good hand lens), a decent set of calipers and a good single-lens reflex (SLR) or digital camera to keep a permanent record. As such, gross morphology (including size and shape) has long been a subject of interest to paleoanthropologists. Measurements also have a long-standing role in assessing human evolution (Wolpoff, 1971; Frayer, 1977; Brace et al., 1987; e.g., Bermúdez de Castro and Nicolás, 1996). The assessment of metric variation in living modern humans has also been applied to questions of modern populations (Hanihara and Ishida, 2005). Simple measurements of tooth length and breadth can be used to obtain broad morphological characterizations (e.g., crown indices and crown areas). However, tooth size does not discriminate well between closely related hominin species and appears to be under greater environmental influence than crown morphology (Townsend and Brown, 1978). Consequently, it may be less useful for addressing hominin evolutionary relationships.

The bumps and grooves that make up the tooth surface are more challenging to quantify than are dental metrics. Attempts to quantify morphological variation include the study of relative cusp areas (Wood and Abbott, 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Bailey et al., 2004 Moggi-Cecchi and Boccone, 2007), cusp angles (Morris, 1986; Bailey, 2004), crest lengths (Pilbrow, 2003; 2007), as well as non-metric traits. Discrete, non-metric traits (e.g., shovel-shaped incisors, Carabelli's cusp) have a long history of use in characterizing modern human populations (Hrdlička, 1920; Pedersen, 1949; Turner and Scott, 1977). They have also played an important role in human evolutionary studies (Hrdlička, 1911; Weidenreich, 1937; Robinson, 1954; Grine, 1985; Suwa et al., 1996). However, the systematic study and application of dental non-metric traits to questions of human evolution has grown since standards were developed (Dahlberg,

S.E. Bailey and J.-J. Hublin (Eds.), *Dental Perspectives on Human Evolution*, 3–8.

1956) and made readily available to the public (Turner et al., 1991). These standards have helped to ensure that researchers are all talking about the same thing, facilitating comparative studies of contemporary (Lukacs, 1984; Turner, 1985; Sofaer et al., 1986; Hanihara, 1989; Irish and Turner, 1990; Turner, 1990; Turner, 1992; Irish, 1994; Hawkey, 1998) and fossil (Crummett, 1994; Bailey, 2002b; Irish and Guatelli-Steinberg, 2003) humans.

Some of the issues of interest in human evolutionary studies include assessing intra- and inter-specific variability, identifying and diagnosing taxa, and working out phylogenetic relationships among extinct fossil species. The application of dental morphology to these questions has come a long way since the days when the primary focus was on shovel-shaped incisors and taurodont molars. Researchers have accumulated large quantities of data on many non-metric trait frequencies in living modern humans. There is less information, however, on the morphometric variation among and within extant ape species (Uchida, 1996; Uchida, 1998a; Uchida, 1998b; Pilbrow, 2006). Assessing variation within and between species of extant apes is important if we are to successfully use dental morphology to identify the number of species represented in a particular fossil collection. Here, Pilbrow uses dental morphometrics (length, breadth and crest lengths) as a proxy for morphological variation to examine variation in extant apes. This marks a significant step forward in understanding intra- and inter-specific variation in our closest living relatives, and in making predictions about what we might expect to find in early hominins.

In the 1980s Wood and colleagues investigated dental morphological variation in early (Plio-Pleistocene) hominins using cusp areas and a limited number of morphological traits (Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988). Since then, technological advances (e.g., digital imaging and image analysis) have made the collection and manipulation of large amounts of data more feasible. In addition, many new fossils from this time period have been uncovered.

Bailey and Wood move beyond previous studies of Plio-Pleistocene dental morphology that relied solely on modern human standards (Irish, 1998; Irish and Guatelli-Steinberg, 2003), and incorporate several new traits in their analysis of dental evolution within the hominin clade. They conclude that some of the dental trends (e.g., morphological simplification) said to be characteristic of *Homo* appear relatively late in human evolution. However, a more accurate assessment of hominin dental evolution will come only after scoring standards that incorporate variation observed in Plio-Pleistocene hominins are developed.

Moggi-Cecchi and Boccone use new digital imaging and analysis techniques to assess upper molar morphometric variation of the expanded South African Pliocene fossil hominin record. Their results support trends and characterizations suggested previously by Wood and colleagues, but they also note a great deal of size variability in the expanded *A. africanus* sample. Studies in inter- and intra-specific variation in extant apes (e.g., Pilbrow, 2007) may ultimately help work out the significance of this variation.

The dentition has traditionally played a less prominent role in studies of later human evolution (Middle and Late Pleistocene) than it has in earlier human evolution. This may be because later hominins (e.g., Neandertals) have been assumed to have teeth that are indistinguishable from our own. Recent studies showing that teeth are important tools in assessing later human evolution (e.g., Bailey, 2002a, 2004, 2006; Bailey and Lynch, 2005), as well as the discovery of large samples of well-preserved European Early and Middle Pleistocene fossil hominins have led to a renewed interest in dental variation during this important time period. Here, Martinón-

Torres et al. (2007) use new dental data from Gran Dolina and Sima de los Huesos to explore questions about phylogenetic relationships between these populations, as well as to investigate possible evolutionary scenarios within Europe.

Phenetic assessments, rather than phylogenetic ones, are more commonly the focus of dental morphological study. One standard for assessing biological relationships using dental morphology is the Mean Measure of Divergence (Sjøvold, 1973; Berry, 1976; Harris, 2004). But several other methods for assessing biological distance and modeling dental relationships are available (e.g., Mahalanobis distance). Sample sizes and extent of completeness of the dentitions will play a role in choosing one's method. The Mean Measure of Divergence is used by Bailey and Wood (2007) in their assessment of Plio-Pleistocene dental relationships. Manni et al. (2007) take a novel approach and apply a method derived from artificial neural networks called Self Organizing Maps (SOMs) to assess phenetic relationships among Pleistocene hominins. One advantage of this method is allowing the use of specimens with missing data; in addition it enables one to avoid *a priori* grouping of specimens by analyzing individuals rather than trait frequencies in samples.

Each of the aforementioned studies relies on direct observation or two-dimensional representations of the crown surface. The final two papers in this section focus on new three-dimensional techniques that can be used to image and study not only the crown surface but also the morphology below. Olejniczak et al. (2007) show how micro-computer tomography (mCT) can be used to capture aspects of tooth morphology otherwise unobtainable through non-destructive means (e.g., morphology of the dentine surface, as well as enamel and dentine volumes). They present the methodological parameters relevant to mCT studies of molars, pointing out that while it may be desirable to have the highest resolution and thinnest slice sections possible in some cases (e.g., for taking accurate distance measurements), slice thickness of 10 times the minimum possible provide accurate data on enamel and dentine volumes. They also review the advantages and disadvantages to using this technique.

Gantt et al. present information on another method for producing high resolution images of internal dental structures - high resolution x-ray computer tomography (HRXCT). Like mCT, with the proper software linear measurements and volumetric data on enamel and dentine can be accurately obtained with HRXCT. According to Gantt et al., HRXCT provides higher resolution and permits the use of a greater size range of specimens (it can handle entire jaws and skulls) but otherwise there are few differences between HRXCT and mCT. Gantt et al.'s study of enamel volume using HRXCT agree with previous studies showing the relationship *Gorilla*>*Pongo*>*Homo*>*Pan* e.g., Kono, 2004; Olejniczak et al. 2007).

These new methods - HRXCT and mCT – address two major issues that have beset many paleoanthropological dental studies in the past. First, they allow one to examine morphology below the crown surface by non-destructive means. Second, they provide a more accurate representation of volumetric and linear data than can be obtained from two-dimensional representations of the crown and EDJ. As such, they open up new avenues of research on internal dental morphology of fossil hominins that were not previously possible.

References

Bailey, S.E., 2002a. A closer look at Neanderthal postcanine dental morphology. I. The mandibular dentition. The Anatomical Record (New Anat.) 269, 148–156.

Bailey, S.E., 2002b. Neandertal dental morphology: implications for modern human origins.

Ph.D. Dissertation, Arizona State University, Tempe.

Bailey, S.E., 2004. A morphometric analysis of maxillary molar crowns of Middle- Late Pleistocene hominins. Journal of Human Evolution 47, 183–198.

Bailey S.E., 2006. Diagnostic dental differences between Neandertals and Upper Paleolithic modern humans: getting to the root of the matter. In: Zadzinska, E. (Ed.), Current Trends in Dental Morphology Research. Univeristy of Lodz Press, Lodz (Poland).

Bailey, S.E., Lynch, J.M., 2005. Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. American Journal of Physical Anthropology 126, 268–277.

Bailey, S.E., Pilbrow, V.C., Wood, B.A., 2004. Interobserver error involved in independent attempts to measure cusp base areas of *Pan* M1s. Journal of Anatomy 205, 323–331.

Bailey, S.E., Wood, B.A., 2007. Trends in postcanine occlusal morphology within the hominin clade: The case of *Paranathropus*. In: Bailey, S.E., Hublin, J-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht pp. 3–8.

Bermúdez de Castro, J.M., Nicolás, M.E., 1996. Changes in the lower premolar-size sequence during hominid evolution. Phylogenetic implications. Human Evolution 11, 205–215.

Berry, A., 1976. The anthropological value of minor variants of the dental crown. American Journal of Physical Anthropology 45, 257–268.

Brace, C.L., Rosenberg, K.R., Hunt, K.D., 1987. Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. Evolution 41, 705–720.

Crummett, T., 1994. The evolution of shovel shaping: regional and temporal variation in human incisor morphology. Ph.D. Dissertation, University of Michigan, Ann Arbor.

Dahlberg, A., 1956. Materials for the establishment of standards for classification of tooth characteristics, attributes, and techniques in morphological studies of the dentition. Zoller Laboratory of Dental Anthropology, University of Chicago.

Frayer, D., 1977. Metric changes in the Upper Paleolithic and Mesolithic. American Journal of Physical Anthropology 46, 109–120.

Grine, F., 1985. Dental morphology and the systematic affinities of the Taung fossil hominid. In: Tobias, P. (Ed.), Hominid Evolution: Past, Present and Future. Alan R. Liss, Inc., New York, pp. 247–254.

Hanihara, T., 1989. Affinities of the Philippine Negritos as viewed from dental characters: a preliminary report. Journal of Anthropology Society Nippon 97, 327–339.

Hanihara, T., Ishida, H., 2005. Metric dental variation of major human populations. American Journal of Physical Anthropology 128, 287–298.

Harris, E., 2004. Calculation of Smith's Mean Measure of Divergence for intergroup comparisons using nonmetric data. Dental Anthropology 17, 83–93.

Hawkey, D., 1998. Out of Asia: Dental evidence for affinities and microevolution of early populations from India/Sri Lanka. Ph.D. Dissertation, Arizona State University, Tempe.

Hrdlička, A., 1911. Human dentition and teeth from the evolutionary and racial standpoint. Dominion Dentistry Journal 23, 403–417.

Hrdlička, A., 1920. Shovel-shaped teeth. American Journal of Physical Anthropology 3, 429–465.

Irish, J., 1994. The African dental complex: diagnostic morphological variants of modern sub-Saharan populations. American Journal of Physical Anthropology [Suppl] 18, 112.

Irish, J., 1998. Ancestral dental traits in recent sub-Saharan Africans and the origins of modern humans. Journal of Human Evolution 34, 81–98.

Irish, J.D., Guatelli-Steinberg, D., 2003. Ancient teeth and modern human origins: an expanded comparison of African Plio-Pleistocene and recent world dental samples. Journal of Human Evolution 45, 113–144.

Irish, J.D., Turner, C.G., II, 1990. West African dental affinity of Late Pleistocene Nubians: peopling of the Eurafrican-South Asian triangle II. Homo 41, 42–53.

Lukacs, J., 1984. Dental anthropology of South Asian populations: a review. In: Lukacs, J. (Ed.), People of South Asia. Plenum Press, New York, pp. 133–157.

Manni, F., Vargiu, R., Coppa, A., 2007. Neural Network Analysis by using self-organizing maps (SOMs) applied to human fossil dental morphology: a new methodology. In: Bailey, S.E., Hublin, J-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht pp. 3–8.

Martinon-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Bastir, M., Sarmiento, S., Muela, A., Arsuaga, J.L., 2007. Gran Dolina-TD6 and Sima de los Huesos dental samples: Preliminary approach to some dental characters of interest for phylogenetic studies. In: Bailey, S.E., Hublin, J-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht pp. 3–8.

Moggi-Cecchi, J., Boccone, S., 2007. Maxillary molars cusp morphology of South African australopithecines. In: Bailey, S.E., Hublin, J-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht pp. 3–8.

Morris, D.H., 1986. Maxillary molar occlusal polygons in five human samples. American Journal of Physical Anthropology 70, 333–338.

Olejniczak, A.J., Grine, F.E., Martin, L.B., 2007. Micro-computed tomography of primate molars: methodological aspects of three-dimensional data collection. In: Bailey, S.E., Hublin, J-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht pp. 3–8.

Pedersen, P., 1949. The East Greenland Eskimo dentition. Meddelelser om Grønland 142, 1–244.

Pilbrow, V., 2003. Dental variation in African apes with implications for understanding patterns of variation in species of fossil apes. Ph.D. dissertation, New York University, New York.

Pilbrow, V., 2006. Lingual incisor traits in modern hominoids and an assessment of their utility for fossil hominoid taxonomy. American Journal of Physical Anthropology 129, 323–338.

Pilbrow, V., 2007. Patterns of molar variation in great apes and their implications for hominin taxonomy. In: Bailey, S.E., Hublin, J-J. (Eds.), Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology. Springer, Dordrecht pp. 3–8.

Robinson, J., 1954. Prehominid dentition and hominid evolution. Evolution 8, 324–334.

Sjøvold, T., 1973. The occurrence of minor nonmetrical variants in the skeleton and their quantitative treatment for population comparisons. Homo 24, 204–233.

Sofaer, J., Smith, P., Kaye, E., 1986. Affinities between contemporary and skeletal Jewish and non-Jewish groups based on tooth morphology. American Journal of Physical Anthropology 70, 265–275.

Suwa, G., White, T., Howell, F., 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. American Journal of Physical Anthropology 101, 247–282.

Townsend, G.C., Brown, T., 1978. Heritability of permanent tooth size. American Journal of Physical Anthropology 49, 497–504.

Turner, C.G., II, 1985. The dental search for Native American origins. In: Kirk, R., Szathmary, E. (Eds.). Out of Asia: Peopling of the Americas and Pacific. Canberra, Journal of Pacific History, pp. 31–77.

Turner, C.G., II, 1990. Origin and affinity of the prehistoric people of Guam: a dental anthropological assessment. In: Hunter-Anderson, R. (Ed.), Recent Advances in Micronesian Archaeology, Micronesia Supplement No. 2. University of Guam Press, Mangilao.

Turner, C.G., II, 1992. Sundadonty and Sinodonty in Japan: the dental basis for a dual origin hypothesis for the peopling of the Japanese Islands. In: Hanihara, K. (Ed.), International Symposium on Japanese as a Member of the Asian and Pacific Populations. International Research Center for Japanese Studies, Kyoto, pp. 96–112.

Turner, C.G., II, Nichol, C.R., Scott, G.R., 1991 Scoring procedures for key morphological traits of the permanent dentition: The Arizona State University Dental Anthropology System. In: Kelley, M., Larsen, C. (Eds.), Advances in Dental Anthropology. Wiley Liss, New York, pp. 13–31.

Turner, C.G., II, Scott, G.R., 1977. Dentition of Easter Islanders. In: Dahlberg, A., Graber, T. (Eds.), Orofacial Growth and Development. Mouton Publishers, The Hague, pp. 229–249.

Uchida, A., 1996. *Craniodental Variation Among the Great Apes*. Harvard University, Cambridge.

Uchida, A., 1998a. Variation in tooth morphology of *Gorilla gorilla*. Journal of Human Evolution 34, 55–70.

Uchida, A., 1998b. Variation in tooth morphology of *Pongo pygmaeus*. Journal of Human Evolution 34, 71–79.

Weidenreich, F., 1937. The dentition of *Sinanthropus pekenensis*: a comparative odontography of the hominids. Paleontologia Sinica *n.s.* D, 1–180.

Wolpoff, M.H., 1971. *Metric Trends in Hominid Dental Evolution*. Press of Case Western Reserve University, Cleveland.

Wood, B.A., Abbott, S.A., 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. Journal of Anatomy 136, 197–219.

Wood, B.A., Abbott, S.A., Graham, S.H., 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. II. Mandibular molars – study of cusp areas, fissure pattern and cross sectional shape of the crown. Journal of Anatomy 137, 287–314.

Wood, B.A., Engleman, C.A., 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. Journal of Anatomy 161, 1–35.

Wood, B.A., Uytterschaut, H., 1987. Analysis of the dental morphology of Plio-Pleistocene hominids. III. Mandibular premolar crowns. Journal of Anatomy 154, 121–156.