

Cambridge University Press  
 978-1-107-01145-8 - Anthropological Perspectives on Tooth Morphology:  
 Genetics, Evolution, Variation  
 Edited by G. Richard Scott and Joel D. Irish  
 Excerpt  
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# 1 *Introduction*

G. RICHARD SCOTT AND JOEL D. IRISH

## 1.1 Christy G. Turner II and 50 years of dental anthropology

Although “festschrift” is not in the title of this volume, it should be. A festschrift is “a book honoring a respected person, especially an academic, and presented during his or her lifetime” (Wikipedia). In all respects, this work mirrors that definition. This volume emanates from a symposium organized by the editors in honor of Regents’ Professor Christy G. Turner II (Figure 1.1), held in 2010, Albuquerque, New Mexico, at the 79th annual meeting of the American Association of Physical Anthropologists.

Motivated by the research of Bertram S. Kraus (University of Arizona) and Albert A. Dahlberg (University of Chicago) during his graduate student days (see Chapter 2), Turner decided teeth were the perfect tool to address issues of population origins and relationships. From Kraus, he was inspired to explore the genetic underpinnings of tooth crown morphology. From Dahlberg, he was inspired to utilize and improve observational standards so the field of dental morphology could move beyond its old bugaboo, interobserver error (Turner 1967a; Turner et al. 1991).

From 1970 to 1990, Turner worked on new ranked standards for crown and root trait classifications and scored morphological traits in ca. 30,000 skulls in scores of museums throughout the Americas, Asia, the Pacific, and Europe (in that order). Using the Dahlberg plaques as a foundation, Turner (see this volume) and his students developed many classificatory standards during the 1970s and 1980s, ultimately culminating in the Arizona State University Dental Anthropology System (ASUDAS; Turner et al. 1991). His ultimate goal was not simply to develop standards of observation; instead, it was to use these standards to address anthropological problems on local, regional, and global scales.

*Anthropological Perspectives on Tooth Morphology: Genetics, Evolution, Variation*, eds. G. Richard Scott and Joel D. Irish. Published by Cambridge University Press. © Cambridge University Press 2013.

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Figure 1.1. Regents' Professor Christy G. Turner II.

From the simple foundation of an accessory root on the lower first molar (three-rooted lower first molars, or 3RM1; see book cover and Turner 1971), Turner developed a three-wave model for the peopling of the Americas that led to a collaboration with Joseph Greenberg and Steven Zegura in a paper entitled “The settlement of the Americas: a comparison of the linguistic, dental, and genetic evidence” (Greenberg et al. 1986). For the next 20 years, every researcher who published on colonization of the New World was compelled to discuss it in light of the three-wave model (whether in agreement or not). In the process of scoring thousands of Native American and Asian dentitions, Turner (1990) also found a dichotomy between North Asians (Sinodonts) – the source populations for the Americas – and Southeast Asians (Sundadonts) – the source populations for the Pacific. To the initial chagrin of Japanese physical anthropologists, he used dental morphology to show the prehistoric Jomon peoples were linked to Ainu and not the modern population of Japan; the latter instead came from the Asian mainland about 2,200 years ago (Turner 1976).

Given the enormous number of frequent flier miles he was accumulating, Turner's colleagues and students thought he was trying to look at every dentition on the planet. But alas, there were far too many, even surpassing his zeal for travel and collections research. To extend the realm of dental morphology, he encouraged Joel Irish (1993) to take on the colossal task of African

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dental variation, Sue Haeussler (1996) to observe early and late Siberians and Central Asians and tie them to New World groups, Diane Hawkey (1998) to study early and late samples on the Indian subcontinent, Alma Adler (2005) to observe Scots in the context of northern European dental variability, and Christine Lee (2007) to do in-depth research in China and Mongolia. And those were only his PhD students. Master's degree students were also sent far and wide to pursue regional studies of dental morphology, including Mary Larsen (1978), Lorrie Lincoln-Babb (1999), and Stephen Reichardt (2000) in Native American groups; Kathy Roler (1992) and Jaime Ullinger (2002) in the Middle East; Joshua Lipschultz (1996) in northeast Africa; and Jaimin Weets (1996) in Melanesia. This list only takes into account those students whom Turner supervised as graduate students. His work stimulated many more students to write MA theses and PhD dissertations on dental morphology in not only the United States but Europe and Asia as well.

This volume is in many respects a sequel to *The Anthropology of Modern Human Teeth: Dental Morphology and Its Variation in Recent Human Populations* (AMHT; Scott and Turner 1997). In other regards, it is an expansion. In AMHT, there was a chapter on genetics, but this predated the many developments involving homeotic genes, epigenotypes, and evo-devo in general. There was reference to fossil hominin dental morphology in the epilogue, but that topic fell beyond the expertise of the authors, who never systematically studied fossil dentitions. Some comments were directed at the use of dental morphology in assessing ethnicity in forensic studies and morphological studies of deciduous teeth, but these topics were not developed at the time. The main focus of AMHT was variation in the permanent dentition of recent human populations. In the 15 years since its publication, morphological variation has been pursued to every corner of the earth. The aim of the present work is to turn major topics over to subject area experts who can provide the problems, context, and references for the major divisions of this book on human tooth morphology: genetics and evolution, fossil hominins, and variation in recent human populations. The symposium in Albuquerque was limited to fourteen contributors; the present volume includes twenty chapters to broaden further the topics that fall within the realm of human dental morphology.

## 1.2 Genetics and evolution

For tooth morphology to have any currency in assessing population affinities, individual traits should have a strong heritable basis. Early twin studies suggested that dental morphology and agenesis were hereditary (Bachrach and Young 1927; Montagu 1933; Newman 1940), but the modes of inheritance

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of specific traits remained unknown. One early attempt to ascertain mode of inheritance through a pedigree study focused on Carabelli's trait. On the basis of one large and seven small pedigrees, Kraus (1951:354) concluded that the trait segregated in a manner consistent with "2 allelic autosomal genes without dominance" (i.e., intermediate dominance or codominance). While writing his dissertation, Turner used the Hardy-Weinberg formula and goodness of fit tests to determine whether class frequency distributions were consistent with codominant inheritance. For the most part, traits did conform to expectations; as such, he took the next step and calculated gene frequencies for shoveling, Carabelli's trait, the hypocone, and protostylid. He published two papers in which he calculated "gene frequencies" for dental morphological traits to help measure gene flow (Turner 1967b, 1969). Despite this innovative approach, anthropological geneticists were critical of using population data to determine modes of inheritance, forcing him to change directions.

Knowing how important it was to understand the genetic basis of morphological traits, Turner encouraged students to test modes of inheritance using family data. Three dissertations directed at this issue ultimately concluded that crown traits were quasi-continuous variables with polygenic modes of inheritance (Scott 1973; Harris 1977), with major gene effects suggested for some (Nichol 1990). Although morphological traits could not be reduced to gene frequencies, there was now a rationale for using total trait frequencies for population characterizations and comparisons (cf. Falconer 1960).

Since 1990, the revolution in human genomic analysis and an enhanced appreciation of homeotic genes have greatly altered our perspective on the genetics of tooth morphology. This is evident throughout the five chapters in the section on genetics and evolution. According to the experimental work of Jukka Jernvall and his collaborators, there is no simple one-to-one relationship between a particular dental trait and gene. However, the general attribution of polygenic inheritance is becoming more refined; development is not regulated by many genes – each acting with small effects – but rather a finite number of genes operating in concert. They operate in developmental modules to produce a final form, or phenotype.

Although experimental work on rodents has been generalized to mammalian dental development (Jernvall and Jung 2000), genetic research on humans is still required to address questions relative to human crown morphology. Hughes and Townsend review advances in odontogenesis, including the identification of specific genes involved in dental development. Their primary emphasis is on the contribution of twin analyses to genetic studies of tooth size, shape, and morphology. With extensive biological information on >1,200 Australian twin pairs, they summarize heritabilities for crown size, intercuspal distance, agenesis, supernumerary teeth, and crown morphology, including Carabelli's trait;

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cusps 5, 6, and 7; and the hypocone. The heritability calculated for Carabelli's trait is around 90 percent, a value notably higher than that found in smaller twin studies and one that suggests a strong genetic component for this classic trait. Traditionally, twin studies stopped at heritability estimates, but Hughes and Townsend note how analysis can go beyond  $h^2$  ultimately to identify the genes involved in development.

Guatelli-Steinberg and colleagues demonstrate how developmental genetics can guide research questions in dental morphological studies. Following principles of the "morphodynamic model" (Salazar-Ciudad and Jernvall 2002, 2010), they evaluate the presence and size of Carabelli's trait relative to intercuspal spacing, tooth size, and the hypocone; they also consider trait variability between males and females, antimeres, and metameres. Earlier studies noted relationships between Carabelli's trait expression and tooth size, the hypocone, and protostylid; an understanding of how primary and secondary enamel knots and their activator and inhibitor molecules moderate development of major and minor cusps has greatly advanced our knowledge of crown trait formation, along with the interplay of size and morphology.

Rizk and colleagues present a detailed review of dental ontogeny that includes a discussion of specific genes and gene products in the developmental cascade leading to tooth formation. The primary aim of their chapter, however, is to discuss the advantages of the rapidly advancing field of geometric morphometrics (GM). Applications are reviewed for a wide variety of mammals, especially rodents; however, their specific focus is on the dentition of the Old World monkey *Colobus guerza*. The authors approach phenotype from a different perspective than traditional studies, using GM to focus on the entire tooth row and specific elements within the row rather than conventional measurements. When this approach is applied to mammalian dentitions, including our own, it should greatly enhance our understanding of long- and short-term dental evolution.

As a pioneer in studying the effects of chromosomal nondisjunction on dental development, Alvesalo compares cephalograms and dental casts across a wide range of chromosomal syndromes (e.g., XO, XXY, XYY, etc.) to determine how variations in the number of X and Y chromosomes contribute to crown size, structure, and shape, along with root form and craniofacial patterns. Shovel-shaped incisors, for example, differ between individuals with certain syndromes and both their relatives and the general population. This approach complements the use of twins and families in showing how genes on the X and Y chromosomes contribute to tooth size, shape, morphology, and craniofacial dimensions.

Mizoguchi addresses an issue that has long befuddled dental morphologists. Are the accessory ridges, fossae, cusps, and fused or accessory roots that make

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up the panoply of dental morphological traits subject to natural selection or is their variation a product of chance? Harkening back to the selectionist versus neutralist debates, many of us (cf. Scott and Turner 1997; T. Hanihara, this volume) feel that most variation among recent human populations is attributable to genetic drift and founder effect. Others, including Mizoguchi, feel these variables are either directly or indirectly affected by selection. While it would be difficult to demonstrate that Carabelli's cusp contributes to survival or reproduction, Mizoguchi argues this feature (and others) is tied developmentally to biochemical, climatic, and/or cultural variables that are more demonstrably impacted by selection. The key to this approach is finding how dental traits fit within larger biological complexes that are subject to overt selective pressures.

**1.3 Fossil hominins**

The crown and root morphology of recent human populations can only be fully appreciated in light of earlier hominin ancestors. There are classic works on fossil teeth, such as Franz Weidenreich (1937) on *Sinanthropus pekinensis* and J.T. Robinson (1956) on South African australopithecines, but most early workers described every crest, ridge, and tubercle on each tooth without putting those characteristics into a population context (e.g., normal, rare, common). Wood and his colleagues were among the first to tabulate frequencies for crown and root traits in australopithecines and early *Homo*, providing an invaluable perspective on primitive and derived conditions (Wood and Abbott 1983; Wood and Engleman 1988; Wood and Uytterschaut 1989; Wood et al. 1983).

Taking on the thorny issues of hominid origins and Plio-Pleistocene dental variation, Schroer and Wood describe crown and root traits and form in not only early hominins (*Australopithecus* and *Homo*) but also early fossils that may or may not be hominin (e.g., *Sahelanthropus*, *Orrorin*, *Ardipithecus*, *Kenyanthropus*). In delineating "primitive" and derived traits, they come up with a suite of characteristics that defines the "most recent common ancestor" (MRCA) of modern humans and chimpanzees/bonobos. Their conclusions regarding the hominid/hominin status of various fossils may surprise early "fossil hunters" who have a vested interest in the taxonomic status of their discoveries. For future fossil finds, Schroer and Wood make predictions on what characteristics of postcanine macromorphology should be present in the MRCA of hominines and panins/hominins, as well as in the stem taxa of the gorilla, chimpanzee/bonobo, and human clades.

Over the past 20 years, a confluence of events has resulted in an increased level of interchange between researchers who work primarily with fossil



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hominin dentitions and those who work with recent human populations. For one, the standards outlined by Turner et al. (1991) have been utilized to make observations on Neanderthals (Bailey 2002), Middle Pleistocene hominids from Atapuerca and Sima de los Huesos (Bermúdez de Castro 1988, 1993; Martínón-Torres et al. 2012), and early Pleistocene hominids from Dmanisi (Martínón-Torres et al. 2008). These researchers have discovered, perhaps not surprisingly, that the ASUDAS standards are not always directly applicable to earlier hominins. For the most part, earlier and recent humans express the same traits. The issue is that Neanderthals and *Homo heidelbergensis* dental characters often fall outside the range of the ASUDAS standards, which were based on recent *Homo sapiens* crown and root morphology.

Martínón-Torres and her colleagues describe the large sample of Middle Pleistocene hominin teeth from the site of Sima de los Huesos (SH) in northern Spain. In many respects, the 400,000- to 500,000-year-old teeth from this site show close parallels to later Neanderthals. For example, the classic anterior tooth combination of pronounced shoveling, labial convexity, and *tuberculum dentale* typifies both groups. However, in SH, there is more dental reduction than in Neanderthals, and this involves both tooth size and the loss of cusps. How SH shares some characters with Neanderthals and others with modern humans is an intriguing finding that should stimulate new lines of analysis.

Bailey and Hublin complement the article by Martínón-Torres and her colleagues by addressing the issue of what nonmetric dental traits set *Homo sapiens* apart from earlier species of *Homo* (e.g., *Homo heidelbergensis*, *H. erectus*). Their observations show how far the field has advanced in the past 60 years. Franz Weidenreich (1937) thought incisor shoveling linked *Sinanthropus* (lower cave Zhoukoudien) to modern Chinese. As Bailey and Hublin note, shoveling was ubiquitous in earlier hominids, including Neanderthals and *H. heidelbergensis*. It remains highly variable among modern humans, including pronounced reductions in frequency and expression in Western Eurasians and Africans. One trait that seemingly sets modern humans apart is hypoconulid loss on the lower first and second molars. Four-cusped first and second molars are in a ratio of about 10:80 in most Western Eurasian populations, but the distinctness of these frequencies is offset by relatively high frequencies in the sample from Sima de los Huesos. Tooth size reduction, also seen in modern humans and the SH sample, may be implicated in this similarity. The one trait that sets Neanderthals and SH apart from modern humans is the middle trigonid crest. This trait was not even discussed in *The Anthropology of Modern Human Teeth* because it is so rare in modern humans. In Neanderthals and SH, it is almost always expressed. This distinction is evident not only on the crown surface but also on the dentine-enamel surface. This is the kind of trait that pushes the limits of ASUDAS when applied to the fossil record. Another such

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trait is labial convexity. This is typical and pronounced in Neanderthals and SH incisors but is much less common in modern humans. Even when present in modern samples, it never approaches the level expressed in Neanderthals. The appearance of UI1 double shoveling, which occurs only recently in *Homo sapiens*, could be associated with the reduction of labial convexity.

The final contribution on fossil hominins by Macchiarelli and his collaborators is methodological, with examples to illustrate the potential of microfo-cal X-ray computed tomography. Until recently, researchers were “confined” to external crown and root surfaces. With new technology, we can now view not only the outside but also the inside of a tooth. When this method is more widely adopted, it will revolutionize the field of “virtual dental (paleo)anthropology.” The authors use three test cases to show the advantages of this high tech approach to studying teeth. First, they compare antimeres in a well preserved Neanderthal jaw and come up with highly precise measurements of enamel cap volume, dentine volume, pulp chamber volume, and so on. To demonstrate fluctuating asymmetry using conventional calipers and linear measurements is difficult because of the slight differences between antimeres (also compounded by measurement error). Tomographic methods provide far more precise and replicable measurements. Tomography is also used to compare the components of deciduous and permanent teeth in fossil hominins and recent humans and tackle the complexities of root form. The detailed 3-D renderings that can be produced with this method should lead to new research questions on root form and diet. When microtomography becomes readily available in labs throughout the world, it will produce a whole new world of “virtual teeth” and a new set of questions to match.

#### 1.4 Human variation

When we assembled a group of morphologically inclined scholars to provide papers on recent human dental variation, the goal was to cover as much of the world as possible. To a large extent, this was achieved. Major geographic regions of the world covered include Africa (Chapter 12, Irish), Europe (Chapter 13, Scott et al.), Micronesia (Chapter 14, Nelson), South Asia (Chapter 15, Hemphill), China and Mongolia (Chapter 16, Lee and Zhang), and the New World (Chapter 17, Stojanowski et al.). Lukacs and Kuswandari (Chapter 18) focus on a sample from Southeast Asia using deciduous dental morphology, while T. Hanihara (Chapter 19) uses dental morphology and metrics to address the weighty topic of the origins and dispersal of anatomically modern humans.

The papers in this section are a twofold testimony to the legacy of Christy Turner’s research on dental morphology. First, the researchers use all or part



of the ASUDAS to collect data on extinct and extant populations (except for deciduous teeth where K. Hanihara's standards are still used). Second, they address both large scale and regional questions of population origins and relationships, an approach Turner advocated throughout his career. Irish takes on the issue of sub-Saharan African variation and coins a new term that encapsulates this variation – "Afridont." While there is variation in sub-Saharan Africa, the so-called Bantu expansion from West Africa had a major impact on recent dental variation. Scott and his collaborators describe the dental morphology of Basques in northern Spain who have long been noted for their unique language and distinct genetic markers. While Basques may be a descendant population from the western European Upper Paleolithic as many have proposed, they fail to exhibit any crown or root traits that would set them clearly apart from Indo-Europeans in particular or Western Eurasians in general. South Asians from India, Pakistan, and Afghanistan show linguistic and genetic ties to populations in the Middle East, but this is a Holocene phenomenon. Hemphill shows how dental variables can be used to infer the timing and movement of populations into South Asia. Exploiting one of the dentition's many advantageous characteristics, he analyzes tooth size and morphology in both extinct and extant populations. He finds there is no serious bias in combining dental data from the living and dead and notes that by using tooth size apportionment methods, the analysis of size and morphology provides similar results in delineating population affinity.

Turning to East Asia, Lee and Zhang note how earlier research combined populations across China and Mongolia into a composite sample as if there was little or no dental variation in the region. Although populations are mostly Sinodont, there is still regional variation. This is especially notable in northwest China, where there was an early Indo-European presence in the Tarim Basin. Although dealing with a small sample, Nelson demonstrates that for Micronesians from Palau, it is still possible to recognize their Sundadont origins. The sample has exceptionally large teeth, and they are morphologically aligned with Southeast Asia. Deciduous teeth receive much less attention than permanent teeth in studies of dental morphology, in part the result of the limitations of small sample size in the archaeological record. Lukacs and Kuswandari analyze the crown morphology of deciduous teeth in a Malay sample to determine whether they conformed to a Sundadont pattern. They found Malay teeth were most similar to those of South Asians in some analyses but were more African in others. The limited comparative samples for deciduous teeth make such evaluations difficult, but with increased attention, workers will start taking advantage of the largely untapped potential of deciduous crown morphology.

In their review of New World dental variation, Stojanowski and his colleagues acknowledge the significant contribution that Turner made in using

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dental data to develop models for the peopling of the Americas. However, they challenge the notion that all Native Americans are Sinodonts, as a number of researchers, especially in South America, have observed Sundadont characteristics. Turner has opined that crown wear can make a Sinodont dentition appear Sundadont. Although wear impacts the ability to make morphological observations, as noted by Burnett, Irish, and Fong in Chapter 21, it does not impact roots and even root traits purportedly are in line with Sundadonty rather than Sinodonty. Given the diversity of form in Paleoindian and Archaic crania, it is not surprising there is intercontinental dental variation during these early periods. The authors aver it is time to move beyond Sinodonty and Sundadonty and perhaps this will happen. New methods of analysis and the addition of more traits to augment the ASUDAS should make the issue of New World dental variation more interesting and challenging.

Expanding beyond a single continent, T. Hanihara takes a global view of dental variation and puts it to use in helping resolve the problem of the origins and routes of dispersal of anatomically modern humans. In line with the Irish chapter on Africa, this is the continent that served as the springboard for the peopling of the world. But which route did they take, when did they disperse, and how do these factors impact modern human variation? These are the kinds of broad issues Hanihara addresses. Another question revolves around locating the source population for East/North Asians, or in Turner's parlance, Sinodonts. Turner proposed that Sinodonty originated from a Sundadont base so the likely source of origin would be Southeast Asia. Hanihara, however, finds hints that Central Asia and Siberia may provide additional points of origin for North Asians.

## 1.5 Methods and prospects

Many of us who "know teeth" and get involved in forensic anthropology utilize crown and root morphology to assess ethnicity. This is usually done in conjunction with craniometric and anthroposcopic traits for the sake of thoroughness. For the skeletal biologists who do not specialize in teeth, tooth morphology is at a decided disadvantage compared to craniometrics for two basic reasons: (1) it is easy to train students to take classic craniometric measurements; and (2) it is even easier to plug these numbers into a discriminant function program (e.g., *FORDISC*) and get some idea of geographic affinity (whether correct or not).

Edgar and Ousley try to level the playing field for using dental morphology in forensic cases, but this is a work in progress. Using a variety of complex statistics, they arrive at relatively high levels of accurate classification when trying to sort out the basic components of the U.S. population (Euro Americans,