1 Dental Anthropology and Morphology

Introduction

Physical anthropology focuses on human biological variation through time and space. Except for those who work in primate paleontology, hominin origins set the temporal bounds of the field some five to eight million years ago, and extend across time through a diversity of fossil species to modern members of *Homo sapiens*. The geographic bounds extend to all parts of the globe habitable by human populations. Methods employed for conducting research on human variation run the gamut from anatomical measurements and observations to physiological parameters and DNA sequencing. The subjects of study are hominin fossils and all human skeletal and living populations. Problems revolve around a multiplicity of questions involving facets of human adaptation, variation, and history.

Dental anthropology is a subfield of physical anthropology, although many contributors to this area of research come from fields outside of anthropology, notably dentistry, genetics, anatomy, archaeology, and paleontology (Hillson, 1996; Scott and Irish, 2013; Irish and Scott, 2016; Guatelli-Steinberg, 2016). Although dental anthropology strikes outside observers as a specialized field of inquiry, it encompasses a broad range of subjects which, in turn, invite finer levels of specialization. Some workers concentrate on developmental aspects of the dentition, from tooth germ formation to developmental defects of the crown (Hillson, 2014). Others focus on post-eruptive changes such as functional crown wear and culturally prescribed dental modification (Lucas, 2007; Burnett and Irish, 2017). The study of dental pathologies, such as caries, periapical infections, patterns of tooth loss, and periodontal disease, provides another avenue of research (Watson et al., 2010; DeWitte and Bekvalac, 2011; Lukacs, 2011; Willis and Oxenham, 2013). Researchers interested in elements of the human dentition that have some underlying genetic basis study tooth size, morphology, and number (Cadien, 1972; Bailit, 1975; Brook, 1984; Scott and Turner, 1988; Kieser, 1990; Scott, 1992, 2008; Townsend et al., 1994; Hughes and Townsend, 2013; Brook et al., 2014a, 2014b; Hughes et al., 2016).

Evidence accumulated over the past century indicates dental development is regulated to a significant extent by the action of genes (Chapters 3 and 4). This is true

not only for crown and root form in general but extends to the myriad of positive and negative structural variants of a tooth. Dahlberg (1951:140) noted that:

> All human dentitions are basically the same. The differences between individuals are in the number and extent of the primary and secondary characters of the tooth groups, which in turn are the reflections of the genetic constitution of the individual.

From the basic blueprint, or "master dental plan" that characterizes all human dentitions, teeth exhibit morphological and metrical traits that vary within and between populations. From an evolutionary standpoint, these traits are observable in living and fossil hominoids and hominins (Gregory and Hellman, 1926; Weidenreich, 1937; Robinson, 1956; Wood and Abbott, 1983; Wood et al., 1983, 1988; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Bailey, 2002; Bailey et al., 2009; Martinón-Torres et al., 2007, 2008, 2012; Liu et al., 2015). In recent human populations, patterned geographic variation is evident in both tooth morphology and crown size.

The enamel which covers a tooth crown is the "hardest" part of the body, consisting primarily of calcium hydroxyapatite [$Ca_{10}(PO_4)_6(OH)_2$] (Nanci, 2012). Because this inorganic component is extremely durable, teeth show excellent preservation in most taphonomic contexts. In hominin fossil localities and recent archaeological sites, they are often the best-represented remains. It is common to find isolated teeth when the rest of a skeleton has long since disintegrated. In addition to their qualities of preservation, teeth provide the only hard tissues of the human body directly observable in living individuals. They can be studied through direct intraoral examination (open wide please!), but it is more efficient to replicate teeth in the upper and lower jaws through negative alginate impressions that serve as molds for pouring fine-grained plaster, yielding permanent casts or study models. Some workers, especially those in Russia, make observations directly on negative wax bite impressions. Extracted teeth from the living are another venue for study but, given their isolation from the context of the whole dentition, they are less useful than dental casts and human skeletons for a systematic analysis of dental variation.

Dental Anatomy and Dental Morphology

Dental morphologists study the structure and form of teeth. In studies of the human dentition, there are two distinct approaches to crown and root morphology. When dental anatomists write about tooth morphology, they are concerned primarily with normative tooth form (cf. Wheeler, 1965; Carlsen, 1987; Nelson, 2015). For example, the human dental formula of 2-1-2-3, shared by all catarrhine primates (Old World monkeys, apes, and humans), refers to the number of different types of teeth in each quadrant of the upper and lower jaws. In each jaw, humans have four incisors, two canines, four premolars, and six molars with paired teeth on the left and right sides (i.e., antimeres) showing mirror imagery. Human tooth crowns consist of smaller elements referred to as cusps which are augmented by regularly occurring occlusal and marginal ridges. Grooves or fissures of varying depths divide a tooth into its constituent

cuspal and ridge components. Although opposing teeth in the two jaws (e.g., an upper right first molar and a lower right first molar) show size and form differences, incisors can be characterized as spatulate, canines as single-cusped (cuspids) and conical, premolars as two-cusped (bicuspids), and molars as multi-cusped. Similarly, the incisors and canines can be characterized as single-rooted while the upper and lower molars have three and two roots, respectively. Lower premolars usually have single roots, although a normative characterization of root number for upper premolars would depend on the geographic locale of the dental anatomist (e.g., one root in Greenland, two in Nairobi). Although cursory in detail, this is the fundamental blueprint for the human dentition (see Chapter 2 for details). Dental anatomists focus on this blueprint. Their texts are designed to show students the typical, or normative, form of each individual tooth. While they illustrate variant forms of crowns and roots, such variation is of secondary importance (Nelson, 2015). Dental faculty want students to be aware of the variety of morphological structures they might encounter in their practices (at least in "European" dentitions), but subtle differences in crown and root morphology do not ordinarily hamper clinical applications of dentistry.

Two types of morphological variants are observable in the human dentition. The first type involves major deviations from the basic dental blueprint (Fig. 1.1). Adjacent teeth are sometimes fused together, or twinned. Supernumerary teeth, as additions to

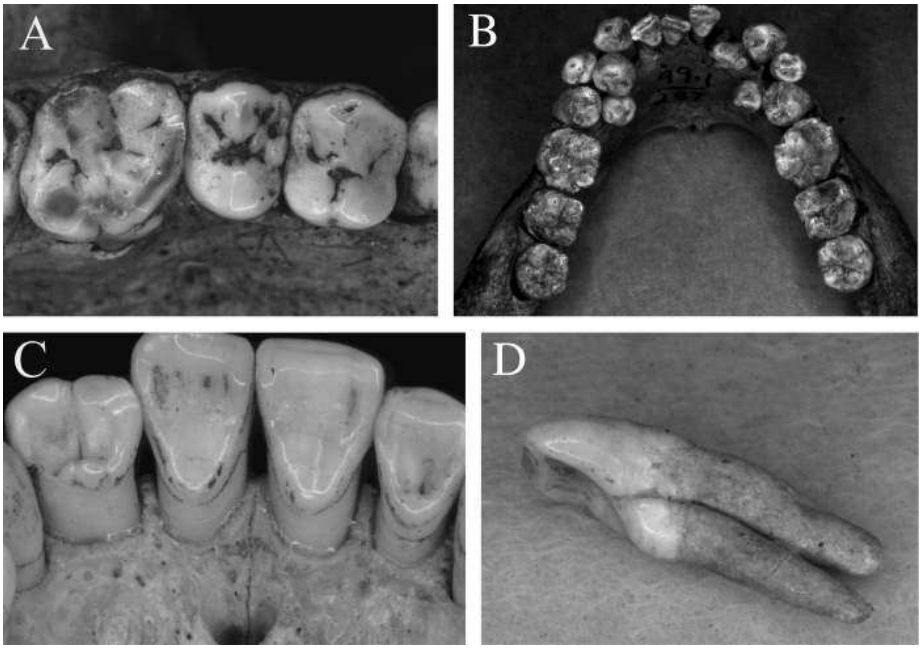

Fig. 1.1 Dental anomalies of rare occurrence: (A) three-cusped upper first premolar; (B) hyperdontia – multiple supernumerary premolars in a lower jaw; (C) a twinned (gemmate) upper right lateral incisor; (D) "hitching a ride" – a supernumerary tooth fused to the lingual base of an upper lateral incisor; not a two-rooted upper incisor. (All photos from C.G. Turner II collection.)

the 2-1-2-3 dental formula, may be normal or anomalous in form and appear either as separate structures or they may be fused to other teeth. While fewer than 5% of the members of a population exhibit extra teeth (i.e., hyperdontia), it is more common for individuals to be missing one or more teeth (i.e., agenesis or hypodontia). Other significant departures from normative crown form include conical lateral incisors, three-cusped upper premolars, "mulberry" molars, and sundry anomalies.

The second type of dental variation is more subtle than twinned teeth, extra or missing teeth, and anomalous crown forms. It involves minor variations in secondary cusps, fissure patterns, marginal ridges, supernumerary roots, and so forth. These minor variants are common and vary within and between populations. They are of greater evolutionary significance than rare and idiosyncratic dental anomalies that are often induced by environmental or epigenetic factors during development. As Butler (1982:44) noted, "The paleontological record indicates that dental evolution proceeds by the selection of minor variations. Presumably, large departures from the normal pattern would be functionally deleterious." While major dental anomalies are interesting and eye-catching, it is minor variations in human dental morphology that are useful in historic and forensic contexts.

The types of dental morphological variation we focus on are largely independent of tooth size, the subject matter of odontometrics (Kieser, 1990; Chapter 3). Our interest is in the secondary structural variants of tooth crowns and roots that are manifest in two primary ways: as "all-or-none" characters (accessory ridges, supernumerary cusps and roots, furrow patterns) or as differences in form (variation in curves and/or angles). The primary focus of this volume is on non-metric crown and root traits that may be either present or absent within any individual dentition. Despite the presence–absence dichotomy, they are not literally all-or-none traits. Within a population, these traits show variation in degree of expression, often noted by such terms as slight, moderate, and pronounced when present. There are also major differences in trait frequency and expression between populations, and it is this variation that is of special significance to physical anthropology and allied fields.

A Brief History of Dental Morphological Studies

In the nineteenth century, dental anatomists and anthropologists described morphological variants and commented on their relative frequencies in different populations. Georg von Carabelli (1842) described an accessory mesiolingual cusp on the upper molars that appeared commonly in European dentitions. At the time, von Carabelli had no idea he would achieve a degree of immortality based on this obscure accessory cusp that bears his name to this day. Early French and German anthropologists and odontologists showed that some morphological variants, such as cusp number of the upper and lower molars, distinguished the major races of humankind. Dental anatomists, including C.S. Tomes (1889), described human crown and root variants and put them in the perspective of comparative odontology. Despite these efforts, by the beginning of the twentieth century, only a small foundation for the systematic study of the evolution and variability of human tooth morphology had been developed.

Aleš Hrdlička (1920a) wrote what might arguably be considered the foundation paper on the study of human tooth crown morphology in his detailed assessment of shovel-shaped incisors (so named because lingual marginal ridges enclose a fossa, giving the tooth an appearance of a "coal shovel"). With access to diverse archaeologically derived human skeletal collections in the U.S. National Museum of Natural History, Hrdlička had an advantage over his European contemporaries. While building on the observations of earlier dental workers, Hrdlička was the first to classify the degree of expression of a morphological variant, assess this variation among several human populations, and describe its occurrence in non-human species. He found a close similarity between Asians and American Indians and their decided difference from European and African populations in the frequency and degree of shoveling expression. In retrospect, this might seem a small point, but this observation was made at a time when the origin of Native Americans was far from resolved. His follow-up article on "Further studies of tooth morphology" (Hrdlička, 1921) extended his observations to other types of morphological variants, but this paper had less impact than the first, perhaps because he provided no methodology for observing these variants and little comparative data were provided to show differences among the major geographic races.

In his opus, *The Origin and Evolution of the Human Dentition*, eminent paleontologist and comparative odontologist W. K. Gregory (1922:476) noted: "apart from a few striking cases, presently to be noted, racial characters in the teeth are not very conspicuous." Influenced in part by Hrdlička's earlier observations on human dental morphology, Gregory felt that, Europeans aside, differences in dental morphology were minor among the varied races of man. The morphological variables considered noteworthy by Gregory included shovel-shaped incisors, *tuberculum dentale* of the upper anterior teeth, upper and lower molar cusp number, lower molar groove pattern, including his *Dryopithecus* Y5 pattern, and the cusp of Carabelli (Chapter 2). Speaking from the vantage of the early twentieth century, Gregory characterized morphological traits as either low characters (i.e., primitive) or high characters (i.e., civilized). His low characters included central incisor shoveling, a molar cusp formula of 4-4-4/5-5-5, Carabelli cusp on M^1 and M^2, and retention of the *Dryopithecus* pattern (Y5) in the lower molars. High characters, or those associated with a so-called modern dentition, included the absence or diminution of shoveling, the rarity of Carabelli cusp, rounded and three-cusped upper second molars, and lower molars with + rather than Y patterns. In this effort, Gregory anticipated the methods of cladistics that emphasize the importance of primitive and derived traits in disentangling evolutionary history.

In 1925, T. D. Campbell published *The Dentition and Palate of the Australian Aboriginal*. He noted that:

> the differences between the dentitions of various types of mankind have not yet been sufficiently recognized to incite very special investigation. But this is probably due, not so much to lack of obvious differences, as to the paucity of specialized study (Campbell, 1925:1).

Campbell covered a wide array of dental topics, including morphological observations on upper and lower molar cusp number, upper premolar and molar root number, and the Carabelli trait. He mentions shovel-shaped incisors but provides no data, adding only that it is not characteristic of the Australian Aboriginal dentition. Noting the preoccupation of his contemporaries with craniology, Campbell (1925:vii) shows prescience in his comment that "a close and detailed study of the dentition and its associated structures does not seem to have attained the position of importance it will undoubtedly gain as time goes on." His monograph was one turning point in that direction.

J.C.M. Shaw (1931), inspired by Campbell's work, contributed the important treatise *The Teeth, the Bony Palate and the Mandible in Bantu Races of South Africa*. Modeling this volume after that of Campbell, Shaw provided morphological observations on upper and lower molar cusp and root number, lower canine and premolar root number, and shovel-shaped incisors. With the publication of Shaw's volume, workers now had baseline data on South Africans as well as Australian Aboriginals. While lauding Shaw's contribution, Sir Arthur Keith notes in the foreword that:

> from the anatomist's point of view the greater part of the world still remains in a state of dental darkness. Even in Europe and America much still remains to be done to complete a preliminary survey of the mouths of mankind.

Despite the urging of Campbell and Keith for physical anthropologists to place more emphasis on the study of dental variation, their advice went largely unheeded. Granted, papers on human dental morphology appeared during the 1920s and 1930s, but these were limited in number and scope. Of special note are Krogman's (1927) long review article on anthropological aspects of the human dentition, Hjellman's (1929) paper on lower molar cusp number and groove pattern, and Tratman's (1938) observations on three-rooted lower first molar variation. Published during this era were dental morphological studies of specific groups, including Hawaiians (Chappel, 1927), Finns (Hjelman, 1929), Bushmen (Drennan, 1929), Japanese (Yamada, 1932), and American Indians (Nelson, 1938).

By 1940, we see the emergence of more intensive interest in comparative dental morphological variation. Two key workers of the time were Albert A. Dahlberg of the University of Chicago and P.O. Pedersen of the University of Copenhagen. Both scholars were dentists whose passion for research carried them to the study of non-European populations. In Dahlberg's case, his work on the morphology of Chicago white dentitions was expanded to American Indians with a primary emphasis on tribal groups in the American Southwest. Dahlberg's in-depth research on one of these groups, the Pima Indians of central Arizona, spanned a 35-year period. During this time, he and his wife, Thelma, amassed several thousand dental casts and associated genealogical records. Among Dahlberg's major early publications were "The changing dentition of man" (1945a), in which he applied Butler's field concept to the human dentition (Chapter 3), and "The dentition of the American Indian" (1951), which provided valuable comparative data for this group. In 1956, Dahlberg released a series of reference plaques to help standardize observations on

morphological variables of the tooth crown. The plaques, with ranked scales for quantifying trait expression, were distributed to workers throughout the world. The plaques for shovel-shaped incisors, Carabelli trait, the hypocone, and the protostylid played a significant role in stimulating further morphological studies of the human dentition.

At the time Dahlberg was systematizing research on American Indian dental morphology, P.O. Pedersen was completing field and laboratory research on living and sub-fossil Greenlandic Eskimos. His monograph *The East Greenland Eskimo Dentition* (1949) has been a primary reference for comparative data since its publication. Pedersen's vast knowledge of the European dental literature provided a bibliographic starting point for many later students of crown and root morphology. Dental research on Arctic populations received another important contribution in 1957 with the publication of C.F.A. Moorrees' *The Aleut Dentition*. Thus, in less than a decade, Eskimo-Aleuts moved from a position of obscurity to a position of prominence in dental anthropological and morphological studies.

There was an active program of dental anthropological research in Japan during the first half of the twentieth century, but until the 1950s the dissemination of this research to western scholars was hampered by language barriers. Early workers, including E. Yamada, T. Fujita, and T. Sakai, helped set the stage for K. Hanihara to develop a strong tradition of dental morphological research among Japanese anthropologists that has thrived over the past six decades, as the following chapters attest.

The decade of the fifties marks a crucial formative stage in the development of dental anthropological and morphological studies. Complementing the work of Dahlberg, Pedersen, Moorrees, and K. Hanihara, B. Kraus contributed foundation papers on the genetics and morphogenesis of tooth crown traits, G. Lasker reviewed the genetic aspects and forensic potential of dental morphology, S. Garn initiated studies on interactions in the dentition, and H. Brabant began important comparative studies of European dentitions from Upper Paleolithic to recent times.

The study of human dental variation received a major boost with the publication of *Dental Anthropology* (Brothwell, 1963). While all facets of dental anthropology were covered in this volume, from odontometrics and crown wear to morphogenesis, also included were important dental morphological papers on shoveling variation (V. Carbonell), the American Indian dentition (A.A. Dahlberg), two-rooted lower canines (V. Alexandersen), and third molar agenesis (D.R. Brothwell). The recognition of dental anthropology as a subfield of physical anthropology is coincident with the publication of this work. After almost 40 years, Campbell's (1925:vii) plea that "The subject of Dentition can no longer be considered one of only incidental interest, but must and will take its place as an important branch of the science of Physical Anthropology" was realized.

In the mid-1960s, A.A. Dahlberg and P.O. Pedersen felt the need for more international communication among members of the dental community who shared a common interest in tooth morphology. To that end, they organized, with the aid of V. Alexandersen, the first International Symposium on Dental Morphology, held

in Fredensborg, Denmark, in 1965. The contributors to this symposium included anthropologists, dentists, geneticists, embryologists, and paleontologists. The overarching theme of the symposium was the structure, function, development, and evolution of teeth. To paraphrase W.K. Gregory, contributors covered the broad scope of dental variation and evolution "from fish to man." The original symposium proved so successful that it spawned subsequent symposia, which have since been held every three years. Proceedings of these symposia, published as edited volumes, include many valuable papers on human dental morphology (Pedersen et al., 1967; Dahlberg, 1971a; Butler and Joysey, 1978; Kurtén, 1982; Russell et al., 1988; Smith and Tchernov, 1992; Moggi-Cecchi, 1995; Radlanski and Renz, 1995; Mayhall and Heikkinen, 1999; Brook, 2001; Żądzińska, 2005; Koppe et al., 2009).

In the past five decades, the number of journal articles and dissertations focusing on dental morphology far exceeds the total for the preceding 100 years. This era has witnessed the classification of many "new" morphological traits, characterizations of numerous population samples, and more concerted efforts to understand the biological nature of crown and root traits. In the description and analysis of human dental variation, researchers from many countries are extending these efforts to all corners of the globe. Geographically, blank spaces remain (Chapter 5) and much remains to be done, but the "state of dental darkness" described by Keith over 90 years ago is slowly emerging into the light. From the 1990s to the present, advances in understanding the evolutionary and developmental processes underlying dental features (i.e., evo-devo), complemented by the emergence of genomics, have moved the study of dental morphology to a new plateau.

Dental Morphology and Physical Anthropology

As physical anthropology embraces the study of primate, hominoid, and hominin evolution, it is impossible for authors to ignore teeth in textbooks on introductory physical or biological anthropology. Many of these texts, however, limit their comments on teeth to broad topics such as heterodont versus homodont dentitions, primate–human differences, tooth eruption in primates, Australopithecine teeth, and the like, but make no mention of dental morphological differences among recent human populations (Lasker, 1976; Bennett, 1979; Eckhardt, 1979; Harrison et al., 1988; Staski and Marks, 1992; Stanford et al., 2013). Other texts include brief mention of morphological differences among modern humans, but these are limited to one or a few sentences on the Asian–European contrast in shovel-shaped incisors (Kelso, 1974; Brace and Montagu, 1977; Weiss and Mann, 1978; Larsen, 2008), the *Dryopithecus* Y5 pattern (Williams, 1973; Poirier et al., 1994), or taurodontism (Birdsell, 1981). A more substantive note is made by Stein and Rowe (1993), who devote a side-bar to the congruence between language phyla and tooth morphology among Native Americans and discuss the implications of this finding for the peopling of the New World.

Textbooks specifically addressing human racial variation devote slightly more attention to dental morphology than introductory texts. In C.S. Coon's (1965) *The*

Living Races of Man, the index has many items listed under "Teeth," but a close perusal turns up mostly references to large-toothed or small-toothed populations. Coon does, however, refer to shovel-shaped incisors in three contexts. First, he says in his characterization of Mongoloids that "The incisors are often, if not usually, 'shovel-shaped'; that is concave behind" (Coon, 1965:11). Second, he notes the Ainu show less shoveling than Mongoloids, a point he uses to support the notion that this group was of Caucasoid or "archaic Caucasoid" descent (Coon et al., 1950). Finally, he takes issue with Osman Hill (1963), who proposed Upper Paleolithic Europeans settled the New World. Coon (1965:151) felt this position was untenable, remarking that, "One objection to his hypothesis is that the American Indians have a much greater incidence of shoveled incisors than any Asiatic peoples, and in more extreme forms." Europeans, by contrast, exhibit a much lower frequency of shoveling and even when the trait is present, it is more muted in expression.

An author who made significant contributions to dental genetics and anthropology, S.M. Garn (1971), devoted two pages to the "variable dentition" in *Human Races*. Regarding morphology, he notes shovel-shaped incisors are common in American Indians, and are present, though less common, in Polynesians, Finns, and fossil hominins. He says some groups show a reduction in cusp number (e.g., Middle Easterners) while others have increased cusp numbers (e.g., Australians, Melanesians). His first reference is to an elevated four-cusped lower molar occurrence in Middle East populations, although he is not specific on how Australians and Melanesians have increased cusp number. Garn also presents a histogram showing the population variation of Carabelli trait.

In *Races, Types, and Ethnic Groups*, S. Molnar (1975) refers to dental morphological variation and provides a table on shoveling variation. After showing how shoveling divides the world into "haves" and "have-nots," Molnar (1975:61) states:

> Several other features of the dentition show a great deal of variability and, in some cases, have been grouped according to race. More often, though, there is only a variability in the frequency of the occurrence of the particular trait, with all the major groups of mankind possessing it to some degree.

Given this situation, he adds that several features must be assessed in any study of population affinity. We agree with both points. Human population variation in dental morphology is a question of degree, not kind, and it is essential to consider as many variables as possible in microevolutionary and historical studies. However, his qualification seems unnecessary given that no single biological trait or gene divides the world's many populations in a historically valid way. Why should teeth be any different?

A.M. Brues (1977), whose research interests did not involve teeth, devoted three pages to the topic in *People and Races*. Part of her discussion focused on crown wear, dietary behavior, and caries in modern populations, but she also addressed variation in tooth size and third molar agenesis. Regarding dental morphology, she described the variation in shovel-shaped incisors and concludes: "The shovel incisor is as clear a racial marker as numerous traits often considered to be of primary racial

significance" (Brues, 1977:136). She also remarks that Carabelli's trait "in its more marked manifestations is virtually limited to Caucasoids" (Brues, 1977:137). The view that shoveling = Asians and Carabelli's trait = Europeans is deeply entrenched in anthropological thinking, even though it is not correct (Chapter 5). The most telling comment made by Brues (1977:137) is: "Other variations of cusp patterns of teeth are interesting to specialists, but we will pass them over."

Biological anthropologists who practice in non-dental branches of the subdiscipline have long adopted the tack of "passing over" dental morphological traits. Shovel-shaped incisors have received sufficient recognition over the years and if any dental trait is mentioned in an introductory course, it is almost assuredly shoveling. Shoveling is a very useful trait, but we show in the following chapters that it is only one of many morphological variables that exhibit a distinctive pattern of geographic variation.

Dental morphological traits do not vary without reason across the landscape in some higgledy-piggledy fashion. Tooth morphology is part of the biological heritage that humans carry with them when they migrate, much like their blood group genes, fingerprint patterns, phenylthiocarbamide taste reactions, and other biological traits. When human groups are isolated from one another for a period, their crown and root trait frequencies diverge to varying degrees, depending on population size and the extent and temporal duration of isolation. When divergent populations come in contact and interbreed, the resulting population possesses convergent morphological trait frequencies. In other words, these polymorphic features of the dentition behave like other biological variables that are used to assess population history and evolutionary process. Moreover, their observability in extant populations and availability in the archaeological and fossil record give them almost unique standing among biological traits in the study of short-term and long-term hominin evolution.

Goals and Organization

With the expanding application of dental morphology to anthropological and historical problems, colleagues in anthropology and allied fields have commented that they lack the expertise to evaluate the "dental evidence" proffered for a hypothesis or model. This volume is partly intended to meet this need by providing background on teeth for non-dental specialists who are working on common historical problems. For example, the origin(s) of Native Americans is one classic problem that cross-cuts many disciplines. The three-wave model for the peopling of the Americas developed by C.G. Turner II based on tooth crown and root trait frequencies stimulated collaboration, discussion, and debate among not only physical anthropologists but also archaeologists, geneticists, linguists, and Native Americans themselves. This model is presented in a series of articles (Turner, 1971, 1983a, 1984, 1985a, 1985b, 1986a; Greenberg et al., 1985, 1986), but articles have space limitations, precluding a full explication of underlying methods and assumptions.