INTRODUCTION

This contribution to the literature of paleopathology has three goals: to provide context and perspective on the field of dental paleopathology, giving consideration to its links with allied disciplines, to review select examples of recent advances and enduring problems in the field, and to identify promising and prospective areas for future research. The introduction contextualizes the study of dental diseases and developmental anomalies in past populations by defining and delimiting this topically broad discipline and by providing historical perspectives on specific issues. Significant trends and accomplishments are noted and critically evaluated. The review of recent research achievements and enduring problems confronting the field focuses on four topics: a) dental diseases and anomalies in pre-Holocene hominins, b) diet, subsistence and dental disease, c) advances in caries research and sex differences in etiology, and d) developmental and genetic dental anomalies. Examples from my own research and from the current literature in dental paleopathology are included. The chapter identifies problematic issues in the field and suggests prospective areas for further research.

This broad, thematic, issues-oriented approach to the study of dental disease in past populations was adopted because existing literature already contains abundant
resources devoted to the recognition, diagnosis, scoring, interpretation and reporting of pathological dental lesions. Some of these resources provide overviews treating multiple lesion types (Lukacs 1989; Langsjoen 1998; Hillson 2000), while others are dedicated to specific lesions: abscesses and granulomas (Dias and Tayles 1997; Ogden 2008), calculus (Lieverse 1999), caries (Lukacs 1995; Erdal and Duyar 1999; Hillson 2001, 2008; Duyar and Erdal 2003), and enamel hypoplasia (Goodman and Rose 1991; Goodman and Song 1999), to cite some examples. Another motivation for pursuing an expansive range of topics is to counter the perception that dental paleopathology is restricted to, or exclusively focused on, issues regarding the relationship between dental disease and diet, nutrition, or subsistence. By defining the field broadly and illustrating the diversity of techniques and applications embraced by dental paleopathology, new ideas and prospects for creative and innovative research will be fostered.

DEFINING AND DELIMITING THE FIELD OF STUDY

Dental paleopathology strives to identify and interpret diseases and anomalies of the teeth and jaws of past populations. The analysis of dental diseases and anomalies is conducted within two broad arenas or research traditions. One tradition is focused on the relationship between dental diseases and cultural factors such as diet, nutrition and subsistence. Another is centered on anomalies of dental development that are influenced to a greater extent by genetic factors. Each of these research traditions has a long and well established history and each has benefitted from research accomplishments of both anthropologists and clinical investigators.

Within the diet and dental disease research paradigm a diverse array of specific goals motivate research. These include: a) determining subsistence and diet of skeletal series with few associated cultural remains (Turner 1979; Lukacs 1989), b) understanding how differences in food preparation can influence the frequency of pathological lesions (Powell 1985), c) reconstructing trends in oral pathology across major changes in subsistence, such as the shift from foraging to agriculture (Cohen and Armelagos 1984; Cohen and Crane-Kramer 2007), d) determining the impact of colonization on diet and oral health of indigenous populations (Larsen and Milner 1994; Klaus and Tam 2010), and perhaps most commonly, e) providing an integrated biocultural perspective on subsistence, diet and nutrition of past populations. The last objective is an integral component of any multifaceted bioarchaeological research project. The basic data that come from such studies ultimately permits regional and global synthetic analyses of oral health from a comparative, paleoepidemiological perspective.

A second somewhat less common, yet valuable, area of enquiry in dental paleopathology involves genetic and developmental anomalies of the teeth and jaws. The anthropological analysis of developmental and genetic anomalies of teeth entails a wide range of goals and objectives. These include dental morphogenesis and pathogenesis, evolutionary trends and variation in tooth size and number of teeth, how population size and isolation influences breeding systems and the frequency of dental anomalies, physiological stress and developmental dental aberrations, and forensic identification. A comprehensive review of hereditary dental anomalies included anomalies of tooth form and size, disorders of tooth number, anomalies of
tooth position (malalignment) and arch relationship (malocclusion), hereditary disturbance of tooth structure (amelogenesis and dentinogenesis imperfecta), disturbances in tooth eruption, and congenital defects and syndromes involving dental anomalies (Alt and Türp 1998). Recent developments in each of these two major research paradigms will be summarized and critically discussed in the classification of oral diseases, the interdisciplinary nature of research and some important historical issues are considered.

A CLASSIFICATION OF DENTAL DISEASES

The broad subdivision of dental diseases and anomalies into two main research paradigms, dental diseases associated with cultural factors and dental diseases linked to genetic and developmental anomalies, is not always clearly discernable in classifications of dental pathology. Nevertheless, classifications of dental diseases are useful because they define the nature and breadth of pathological conditions and processes studied, and also reveal how limited is the list of diseases and anomalies that can be investigated in ancient skeletal samples. For example, Chapter XI of the WHO’s International Classification of Diseases (2007) is devoted to diseases, disorders and anomalies of the digestive system and includes a “block” (K00-K14) entitled “Diseases of oral cavity, salivary glands and jaws.” An abridged version of the WHO–ICD list of diseases of the teeth, jaws and salivary glands is provided in Table 30.1 to illustrate the range of pathological lesions subsumed under the rubric of dental disease.

While this list is comprehensive, it does not clearly differentiate diseases and anomalies into the two research paradigms described above. The diet and dental disease paradigm includes WHO–ICD disease categories K02 through K06, while the genetic and developmental diseases paradigm would consist of categories K00–01, K07, K09 and K10. Some WHO–ICD categories consist exclusively of soft tissue pathological conditions, such as stomatitis, and diseases of the lip, oral mucosa, and tongue (K12–14), and therefore cannot be studied in skeletal samples. Other categories (K08, for example) include a mix of systemic and genetic conditions (exfoliation) with lesions such as tooth loss that may be secondary to nonsystemic factors including injury or diseases with a dietary association (periodontal disease, scurvy).

Clearly, dental paleopathology as a field of research is interdisciplinary in nature and derives significant methodological and theoretical input from anthropology, dentistry and evolutionary biology (see Figure 30.1). Depending on the nature of the research problem, dental paleopathology benefits from methodological and theoretical developments in many allied fields. For example, ethnographic documentation of diet and food preparation methods may provide indispensable contextual data for better understanding differences in the frequency of pathological dental lesions. Use of teeth as tools in a wide range of nondietary occupational tasks, such as the use and making of tools or processing of reeds or sinew, is enhanced and amplified by ethnographic research (Larsen 1985; Brown and Molnar 1990). An ethnographic component in the assessment of diet, dental health and culture change has been adopted by Walker and colleagues in the study of African hunter-gatherers (Aka, Mbuti) and their farming neighbors, the Bantu (Walker and Hewlett 1990). Subsequently, investigations among South American native hunter-horticulturalists,
Table 30.1  World Health Organization’s International Classification of Disease

<table>
<thead>
<tr>
<th>Block  K: Diseases of oral cavity, salivary glands and jaws</th>
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<tr>
<td>K00 Disorders of tooth development and eruption</td>
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<tr>
<td>Anomalies of number, size and form; mottled teeth; enamel hypoplasia; peg-shaped teeth; enamel pearls; hereditary disturbances of tooth structure.</td>
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<td>K01 Embedded and impacted teeth.</td>
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<td>Failure to erupt with (impacted) or without (embedded) obstruction.</td>
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<td>K02 Dental caries</td>
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<td>Caries of enamel, dentine, cementum.</td>
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<td>K03 Other diseases of hard tissues of teeth</td>
</tr>
<tr>
<td>Excessive attrition, abrasion, erosion; hypercementosis; calculus; accretions.</td>
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<tr>
<td>K04 Diseases of pulp and periapical tissues</td>
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<tr>
<td>Pulpitis, abscesses, radicular cysts.</td>
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<tr>
<td>K05 Gingivitis and periodontal diseases</td>
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<tr>
<td>Acute and chronic gingivitis, periodontitis.</td>
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<td>K06 Other disorders of gingiva and edentulous alveolar ridge</td>
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<tr>
<td>Gingival enlargement or recession, alveolar ridge lesions associated with trauma.</td>
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<tr>
<td>K07 Dentofacial anomalies [including malocclusion]</td>
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<tr>
<td>Anomalies of arch position, tooth position, temporomandibular joint disorders.</td>
</tr>
<tr>
<td>K08 Other disorders of teeth and supporting structures</td>
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<tr>
<td>Exfoliation from systemic cause, tooth loss from injury, extraction, periodontitis.</td>
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<tr>
<td>K09 Cysts of oral region, not elsewhere classified</td>
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<tr>
<td>Developmental, odontogenic and non-odontogenic cysts.</td>
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<tr>
<td>K10 Other diseases of jaws</td>
</tr>
<tr>
<td>Maxillary and mandibular tori, Stafne’s cyst, exostoses, osteitis, periostitis.</td>
</tr>
<tr>
<td>K11 Diseases of salivary glands</td>
</tr>
<tr>
<td>Atrophy / hypertrophy of salivary gland, gland stones and calculus, xerostomia.</td>
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<tr>
<td>K12 Sialodochitis and related lesions</td>
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<tr>
<td>K13 Other diseases of lip and oral mucosa</td>
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<td>K14 Diseases of tongue</td>
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<td><a href="http://apps.who.int/classifications/apps/icd/icd10online/">http://apps.who.int/classifications/apps/icd/icd10online/</a></td>
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</table>

Allied fields contributing to the advancement of knowledge of Dental Paleopathology

**Anthropology**
- Archaeology
- Bioarchaeology
- Ethnography
- Human biology
- Palaeoanthropology
- Taphonomy

**Clinical Dentistry**
- Anatomy & histology
- Development
- Epidemiology
- Genetics
- Evolutionary theory & genetics
- Darwinian medicine (dentistry)

Dental paleopathology

Figure 30.1 Allied fields contributing to the advancement of knowledge of dental paleopathology.
made extensive use of ethnographic data on gender differences in behavior and oral health, diet and food preparation (Walker et al. 1998). In this study investigators stressed the need for more extensive "ethno-bioarchaeological" research, "By this we mean studies in which ethnographic and physical anthropological data are collected as part of collaborative efforts to answer ethnographic and bioarchaeological questions." (Walker et al. 1998: 381).

**The History of Dental Paleopathology**

A comprehensive history of research in dental paleopathology has not been written. However, the historical development of interactive research in North American bioarchaeology and dental anthropology was reviewed by Rose and Burke (2006), who include dental paleopathology as a central theme (Rose and Burke 2006:323–346). Entitled "The dentist and the archaeologist", this comprehensive historical review includes pathological dental lesions, together with developments in the anthropological study of tooth size, tooth wear (macro- and micro-), microstructure (histology), and morphology, with special attention to ancient North American samples and investigators. In their analysis, the history of dental anthropology is organized into four chronological periods and three stages of research development. Following Willey and Sabloff (1993) the chronological periods include: a) Classificatory / descriptive (1840–1914), b) Classificatory / historical (1914–1940), c) Contextual / functional (1940–1960) and d) Modern (1960–present). Conceptually, the progressive development of research in dental anthropology is viewed as conforming to a general developmental sequence of stages: from plausibility to methodology to application. The stage of plausibility relies on the application of uniformitarian principles to establish that an idea, or cause-and-effect relationship, observed in living groups is also discernable in prehistoric skeletal samples. For example, variation in degree of occlusal wear or nature of striae in modern groups is linked to food consistency or to food-preparation methods. Plausibility establishes that degree of wear in skeletal samples reveals information about food texture and preparation practices in the past. The methodology stage develops and refines standardization of data collection, analytic techniques and interpretation, thereby improving reliability of observations and fine tuning causal associations between diet and dental disease or between frequency of dental anomalies and evolutionary principles such as mating patterns. Application is the third stage in this developmental sequence. Fundamental relationships between cause and effect established during the plausibility and methodology stages can now be applied with reliability and confidence. Application stage goals include either systematically documenting pathological dental lesions or anomalies in archaeologically derived human skeletal series, or addressing specific problem-oriented research questions employing extensive comparative samples.

Rose and Burke's (2006) historical study of bioarchaeology and dental anthropology provides useful insights regarding the development of dental paleopathology; they include a) significant advances made in different subfields by pioneering researchers (Mummery, Ruffer), b) early investigator's preempting of dental wear analysis for the purpose of age estimation, thus precluding this variable from a more
prominent role in dietary reconstruction, and c) emphasizing Brothwell’s role in synthesizing and disseminating research in dental anthropology, thus acting as a catalyst for further research in dental paleopathology.

The origin of the term “dental anthropology” has been attributed to a symposium of the Society for the Study of Human Biology at the Natural History Museum (London; Hillson 2007: xxi). The published proceedings volume of this symposium, entitled Dental Anthropology, was edited by D. R. Brothwell, who has played a central role in the development of the field of dental paleopathology in the Modern Era. The catalytic impact of this volume is clearly demonstrated by Rose and Burke (2006:338–39, 342). While the prominent role of Dental Anthropology is well established, the relative neglect of a volume published ten years earlier by two dentists is paradoxical. The Human Masticatory Apparatus: An Introduction to Dental Anthropology employs principles of evolutionary theory and culture change to understand the current condition of modern human teeth and jaws (Klatsky and Fischer 1953). The growth and development, and the structure and function of the masticatory system are addressed before the authors consider dietary variation and its impact on in the masticatory system. The prime focus of the volume is dental pathology—explaining the prevalence of modern human dental diseases within an evolutionary paradigm. In sequence they consider the causes, incidence and prevention of dental caries, periodontal disease and malocclusion. A causal association between “the rise of civilization” and increasing frequency of dental diseases is a central theme of the volume. Though developments in dental paleopathology are not featured in Scott and Turner’s (2008) history of dental anthropology, the impact of Brothwell’s (1963a) Dental Anthropology is regarded as a stimulus for subsequent research, while Klatsky and Fischer’s (1953) volume, subtitled An Introduction to Dental Anthropology is not mentioned.

What accounts for the significant difference in impact these volumes had on the field of dental paleopathology? The possible answers are diverse yet speculative in nature. Basic differences in format, publisher and distribution may be involved. The Masticatory Apparatus was co-authored by two dentists with evolutionary anthropological interests. It was published by a small press (Dental Items of Interest, Brooklyn, NY), with limited distribution. By contrast, Dental Anthropology, an edited volume with 15 chapters and 18 authors, was published by Macmillan, with a more extensive distribution. When topical coverage is considered, just three chapters of Dental Anthropology focus on aspects of dental pathology (Brothwell et al. on congenital absence, Clement on microstructure and biochemistry, and Brothwell on macroscopic dental pathology), while The Masticatory Apparatus gives extensive attention to caries, periodontal disease, and malocclusion in evolutionary perspective. Possibly the more tightly focused, problem-oriented chapters of Dental Anthropology appealed more to anthropologists than the clinical–evolutionary paradigm of The Masticatory Apparatus, which championed the view that modern levels of dental morbidity result from the rise of civilization. Perhaps Klatsky and Fisher’s “Introduction to Dental Anthropology” was unappreciated by its readership—clinicians and practicing dentists, or its distribution was limited and did not reach anthropologists conducting research in dental pathology. The minimal impact of this volume on the field of dental paleopathology is in some respects surprising and enigmatic.
Brothwell's role in dental pathology, thus acting as a catalyst to a symposium that I organized for the Natural History Museum in London. The focus of this symposium, which has played a central role in the development of modern dental anthropology, is well illustrated by two dentists of the masticatory apparatus—Klatsky and Fisher (1963a) and the change to under-}#THE SCOPE OF DENTAL PALEOPATHOLOGY

Dental paleopathology is a diverse field of research. Hence, different topics within the domain of dental paleopathology appeal to different investigators. As a guide to the literature and for easy reference, frequently cited literature in bioarchaeology and paleopathology has been selected to provide a review of subject matter and topical coverage embraced by the field of dental paleopathology. The goal here is to illustrate the range of subjects, to identify popular topics of research, and to provide a guide to the literature for interested students and researchers. For instance, definitions and current understanding of the etiology of commonly studied pathological dental lesions are provided in Table 30.2, while Figure 30.2 illustrates representative examples of pathological dental lesions commonly recorded in the analysis of dental disease in past populations. Similarly, in Table 30.3, lists dental diseases related to diet, subsistence and cultural modification of teeth along with key sources that address each affliction. While this survey is neither comprehensive, nor complete, it intentionally includes a wide range of publication outlets, from monographs with a geographic or ethnic focus (Bennike 1985; Webb 1995) to book chapters (Lukacs 1989; Hillson 2000); from textbooks in bioarchaeology (Larsen 1997), paleopathology (Roberts and Manchester 2005), and osteology (Mays 1998), to encyclopedia entries (Langsjoen 1998). Historical sources (Klatsky and Fisher 1953; Brothwell 1963b; Wells 1975) and recent publications (Ogden 2008) are also included as well. Differences in topical coverage are remarkable. For example, Mays' (1998) introductory text in human osteology gives attention to two lesion types: caries and enamel hypoplasia; while Roberts and Manchester's (2005) introduction to paleopathology provides extensive coverage of diet-related dental diseases. The paleopathology of Aboriginal Australians specifically avoids dental disease with one exception—dental enamel hypoplasia (Webb 1995). A valuable, yet seemingly underutilized, resource is Langsjoen's (1998) review of dental pathology in the Cambridge Encyclopedia of Human Paleopathology (Auðurheidir and Rodríguez-Martin 1998), which covers a broad range of dental diseases and includes attention to diet-related diseases, genetic and syndromic dental disorders, and cultural modification of teeth. By contrast, Ogden's (2008) chapter on dental pathology centers on of a specific rare type of enamel hypoplasia (cusp and on diagnostic and interpretive problems associated with periodontal disease, abscesses, and granulomas.

Genetic and developmental dental anomalies—(K00-01, K10) are not well covered in most anthropological treatments of dental paleopathology, yet they have considerable significance for understanding evolutionary and population dynamics of earlier human groups. Though not truly "pathological" in nature, evidence of the cultural treatment or modification of teeth is of interest to anthropologists for the insights they yield regarding dental aesthetics in past societies and for the patterning of such practices by gender and status. In addition to the sources in Table 31.3, extensive treatment of topics such as ablation, implants, therapy and occupational wear are discussed elsewhere (Milner and Larsen 1991; Alt and Pichler 1998). Occlusal variation, under the pejorative label "malocclusion," received greater attention among earlier researchers, especially clinically oriented investigators (Brace 1977). An interesting difference in interpreting the etiology of occlusal variation is discernible. Dentists,
Table 30.2 Pathological lesions commonly observed in teeth and jaws of archaeologically derived human skeletons

<table>
<thead>
<tr>
<th>Lesion Type</th>
<th>Definition / Etiology</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td>Abscess</td>
<td>A smooth-walled sinus cavity resulting from chronic infection of the pulp which channels through an exit (fenestra) in cortical bone (periapical / alveolar).</td>
<td>Dias and Tayles 1997, Ogden 2008</td>
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<tr>
<td>Alveolar recession</td>
<td>Reduction in height of alveolar crest due to chronic periodontitis (inflammation of periodontal tissues).</td>
<td>Odgen 2008, Hillson 2000</td>
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<tr>
<td>Antemortem tooth loss</td>
<td>Loss of teeth during life, evidenced by progressive resorption of the alveolus. May result from periodontal disease, penetrating caries, severe occlusal wear or trauma.</td>
<td>Lukacs 1989</td>
</tr>
<tr>
<td>Calculus</td>
<td>Mineralized plaque that accumulates at the basal surface of a living plaque deposit and is attached to the surface of the tooth. Adherence of plaque influenced by biochemical components of saliva.</td>
<td>Hillson 1996, 2000, Lieverse 1999</td>
</tr>
<tr>
<td>Caries</td>
<td>A disease process involving progressive, focal demineralization of dental hard tissues by organic acids derived from bacterial fermentation of dietary carbohydrates, especially refined sugars.</td>
<td>Featherstone 1987, Larsen 1997</td>
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<tr>
<td>Crowding</td>
<td>Displacement of teeth from their standard anatomical position due to inadequate developmental space. Results from a discrepancy between tooth size and jaw size.</td>
<td>Lukacs 1989</td>
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<tr>
<td>Dislocation</td>
<td>Tilting of the tooth (crown lingual / roots buccal) due to progressive loss of support from continuous eruption as a result of severe occlusal wear and alveolar recession. Roots may ultimately remain functional.</td>
<td>Clarke and Hirsch 1991a, b</td>
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<tr>
<td>Enamel hypoplasia</td>
<td>A deficiency in enamel thickness visible as transverse grooves or pits on the outer enamel surface. Results from disrupted ameloblast function and reduced secretion of enamel matrix during amelogenesis.</td>
<td>Goodman and Rose 1991</td>
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<tr>
<td>Granuloma</td>
<td>A small spherical soft-tissue lesion surrounding the root apex (periapical) in which breakdown products of necrotic pulp accumulate creating a space in alveolar bone. (See abscess above.)</td>
<td>Dias and Tayles 1997, Ogden 2008</td>
</tr>
<tr>
<td>Malocclusion</td>
<td>Deviation from a rarely attained ideal arrangement of teeth within and between jaws, not always resulting in functional problems. More appropriately referred to as occlusal variation.</td>
<td>Langsjoen 1998</td>
</tr>
<tr>
<td>Periodontal disease</td>
<td>Inflammation and destruction of periodontal tissues that anchor the tooth to the jaw, results from the accumulation of bacterial plaque at the gingiva (gum margins). Causes reduction in height of alveolar crest.</td>
<td>Odgen 2008</td>
</tr>
<tr>
<td>Pulp exposure</td>
<td>Perforation of the pulp chamber allowing bacterial invasion and contact with connective tissue, nerves and blood vessels. May result from penetrating caries, severe occlusal wear, complicated dental trauma, and other factors.</td>
<td>Langsjoen 1998</td>
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<tr>
<td>Temporomandibular joint (TMJ) disease</td>
<td>An osteoarthritic response to chronic stress of the TMJ, resulting in porosity, marginal lipping or eburnation and altered shape of the articular surface of the glenoid fossa and / or mandibular condyle.</td>
<td>Langsjoen 1998</td>
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</table>
Figure 30.2 Examples of pathological conditions found in human dental remains: a) dislocation of RM, and antemortem loss of teeth due to severe wear (MDH 23); b) antemortem loss (RM3), pulp exposure and periapical abscesses resulting from severe occlusal wear (P4-5, HAR 148a); c) large carious lesion (LM3) exposing pulp chamber (SKH 5); d) medium-size calculus deposits, lingual aspect, left P4 through M1 (SKH 12) (note calculus removed from LM3, only traces present); e) transposed upper left canine. Canine crown carious, large L2-P4 diastema (HAR 156a); and f) linear enamel hypoplasia (LEH) four defects visible in L1. Severe episodes matched on P1, P and C indicating systemic stress (MR2 60) (all photos J. R. Lukacs).

who often treat members of a family from one generation to the next, tend to favor genetic factors. By contrast, anthropologists, who more often combine epidemiological and genetic perspectives in cultural context, find strong environmental factors at work. The epidemiological transition in occlusion can be seen in contemporary groups: with rural communities more frequently exhibiting better occlusion while...
Table 30.3  Tabular guide to topical coverage of oral pathology and related conditions

<table>
<thead>
<tr>
<th>Source</th>
<th>Abcesses</th>
<th>Alveolar resorption</th>
<th>Peridontal disease</th>
<th>AMIL</th>
<th>Calculus</th>
<th>Caries</th>
<th>Evasive wear tooth</th>
<th>Dislocation</th>
<th>Enamel hypoplasia</th>
<th>Hypersensitivity</th>
<th>Pulp exposure</th>
<th>Malocclusion</th>
<th>Crowding</th>
<th>Temporomandibular joint disease</th>
<th>Cultural dental modification</th>
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<td>Bennike (1985)</td>
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urban samples display higher frequencies of malocclusion. A clinial patterning of occlusal variation across the urban–rural continuum is evident in diverse geographical and cultural settings including India (Kaul and Corruccini 1984) and Kentucky (Corruccini and Whiteley 1981), and provides valuable context for understanding the temporal transition in occlusion from past to present (Corruccini 1991). The anthropological analysis of occlusal variation in past populations requires excellent preservation enabling articulation of undeformed upper and lower jaws. While the study of occlusal variation in skeletal samples continues and new methods are being used, the complex biomechanics of occlusion and the impact of severe tooth wear combine to complicate the analysis (Alt and Rossbach 2009).

DENTAL DISEASE IN PAST HUMAN POPULATIONS

Dental diseases and anomalies in pre-Holocene early hominins
This section provides a “deep-time” perspective on diet-based dental diseases (WHO–ICD categories K02 through K06), and on developmental dental anomalies (categories K00-01, K07, K09 and K10). While the primary focus of this chapter is on dental diseases and anomalies of post-Pleistocene, archaeologically derived modern humans, evidence of the longstanding nature of our present-day dental afflictions are becoming better known from the pre-Holocene fossil record. This brief review provides a glimpse of the range of dietary and developmental dental afflictions of early hominins. Representative noteworthy examples include: bilateral temporomandibular joint disease of the mandibular condyles of Australopithecus afarensis (MAK-VP-1/12) from Maka, Ethiopia at 3.4 mya (White et al. 2000). South African early hominins have yielded evidence of a supernumerary upper lateral incisor (SK 83, UI2) and interproximal dental caries, unassociated with enamel hypoplasia, in robust australopithecines at 1.7–1.5 mya (Grine et al. 1990; Ripamonti et al. 1999). Approximately 3.0 percent of a Paranthropus robustus dental sample (over 100 teeth) from Swartkrans has caries lesions, mostly in association with enamel hypoplasia (Grine et al. 1990). While periodontal disease has been reported in Australopithecus africanaus, dental caries have not been documented in this taxon (Ripamonti and Petit 1991; Ripamonti et al. 1997). Dental anomalies and pathological lesions such as axial rotation (90 degrees) of the maxillary left second premolar (D2700), lingual tilting and tesoromolar rotation of the mandibular right third molar (D211), abscesses and periodontal disease (D2600), and edentulism (D3444 / D3900) have been described in the extensive fossil sample of Homo erectus (cf. ergaster) from Dmanisi at 1.7 mya (Lordkipanidze et al. 2006; Rightmire et al. 2006). Bilateral, ninety degree rotation of maxillary P’s has been documented in the enigmatic hominin taxon Homo floresiensis (specimen LB1) (Brown et al. 2004:1058), as well as in living and archaeological samples of modern humans (see Figure 30.3).

While caries are generally rare in pre-Holocene fossils, they have been reported in Neanderthal and early modern human specimens (Brothwell 1965b; Hillson 2008). One unrepresentative yet provocative specimen, the Kabwe skull (Broken Hill 1), exhibits rampant dental caries (with 10 of 16 maxillary teeth affected). In addition, this unique individual exhibits multiple periapical abscesses, exposure of the pulp chamber and secondary (reparative) dentin (Koritzer and St. Hoyme 1979; Sperber
Figure 30.3  Examples of rotation of maxillary P4: a) maxilla, Homo floresiensis (LB 1), showing bilateral rotation of P’s (Brown et al. 2004; photo courtesy of Peter Brown); b) maxillary dentition, adult female (MR3 183) Neolithic Mehrgarh, with bilaterally rotated P’s (photo J. R. Lukacs); c) maxillary dentition (MR3 283), Neolithic Mehrgarh, with bilateral 45 degree rotation of P inferred from interproximal wear facets (photo J. R. Lukacs); and d) maxillary dentition of an adult Chenchu female (CHU 73) with bilateral rotation and reduced crown size of P4 associated with reduced crown size of R4 (photo G. C. Nelson).

The poor oral health of Kabwe has been attributed by some to lead poisoning (Bartzokas and Day 1993) and by others to lack of dental hygiene—specifically not knowing the use of tooth picks (Puech et al. 1980). Developmental anomalies including tooth rotation, supernumerary and congenital absence of teeth, occlusal variation and anomalies of eruption have been documented for Middle Paleolithic early modern humans from Dölni Ve’stonice and Pavlov (Hillson 2006). Finally, the analysis and interpretation of developmental enamel defects known as linear enamel hypoplasia (LEH) in hominin fossils has burgeoned, yielding new insights on the
Holocene changes in subsistence, diet and dental disease: the impact of agriculture

Changes in prevalence of a complex group of diet-related dental diseases (WHO-ICD disease categories K02 through K06) is the main theme of this section. The nature of research conducted by pioneers in the field of dental paleopathology reveals that many questions motivating 21st-century research have long and well-established histories. An early phase in this history involved the recognition that pathological lesions and developmental anomalies in ancient specimens could be equated with diseases and abnormalities in living populations. The study of dynastic Egyptians by medically trained British anthropologists is noteworthy in this regard, with initial studies by Marc Armand Ruffer (1913, 1920; Sandison 1967) and Grafton Elliot Smith and Fredric Wood Jones (Smith and Jones 1910). Both lesion categories, dental diseases relating to diet and developmental genetic anomalies were included in Ruffer's analyses. The study of dynastic Egyptian dental disease continues into the modern era, with the work of Greene (1967, 1972), Hillson (1979), and Forshaw (2009).

While research on diet, subsistence and dental disease has many potential foci, the most intensively investigated question is, "How does a shift in subsistence and related changes in diet impact dental health?" Significant changes in dental health comprise one of several complex and interrelated biological consequences of agriculture and sedentism (Larsen 1995). Key distinctions in dental pathology profile have been documented for hunting and foraging groups and farmers. The foundation for such studies included early "ethno-bioarchaeology" research on the relationship between diet, subsistence and dental disease among native North Americans by (Leigh 1925), which helped provide context for the analysis of diet among prehistoric groups (Leigh 1929). The associations between diet and dental pathology, and to a lesser extent dental wear, were incorporated in the analysis of living groups (Aleur) (Moorrees 1957) and of prehistoric skeletal samples (Pecos Pueblo) (Hooton 1930). The idea that an epidemiological transition in dental health accompanied the subsistence shift from hunting and foraging to agriculture received extensive support in the influential volume Paleoanthropology and the Origins of Agriculture (Cohen and Armelagos 1984). Two theoretical propositions were addressed in this volume: a) that agriculture was not adopted by choice, but rather resulted from need and stress, and b) that the
### Table 30.4 Changing global coverage of health and subsistence transition

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The trajectory of human health following the adoption of farming is better characterized by decline rather than progressive improvement. The idea that the origin and intensification of agriculture was accompanied by an array of biological costs, that could be measured in terms of longevity, stature, physiological stress, relative workload, and oral health was demonstrated in skeletal and dental samples from diverse regions of the globe. Of the 19 studies in this volume, nearly half (47.4 percent) focused on sites and samples from North America (see Table 30.4). Problems of small sample-size and regional representation, uneven coverage of chronological periods and subsistence categories, and diversity of research methods muted the impact of this volume for some. However the consensus regarding dental health was clear—that the transition to agriculture was associated with a decline in oral health. The decline in oral health with farming was patently evident in the increasing frequency of dental caries, but other dental diseases and dental wear were also involved. These findings may derive in part from the North American focus of the volume and the detrimental consequences of maize-dependent diets on general health and nutrition and on oral health in particular.

In April 2004, on the 20th anniversary of the publication of *Paleopathology at the Origins of Agriculture*, an international group of bioarchaeologists convened in Clearwater, Florida at a Wenner-Gren-sponsored symposium to update and reassess skeletal evidence of agricultural and economic intensification (Cohen and Crane-Kramer 2007). Organizers intentionally broadened the geographic diversity of sites and samples with a significant increase in attention to data from Asia appearing in the published volume, *Ancient Health*. While only three chapters (15.8 percent) of the 1984 volume dealt with Asian samples (India, Levant, and southwest Asia) the 2007 update had nine chapters (42.9 percent) on Asia, the majority of these (seven chapters) centered on southern Asian samples (Bahrain, India, Levant, Malaysia, Thailand (2), United Arab Emirates) (see Table 30.4). The relationship between dental health, diet and subsistence received attention from most investigators (17/21 chapters; 81 percent). Perhaps not surprisingly the clear correlation between farming and oral health (especially caries) resulting from the 1984 volume was less clear in the sequel, *Ancient*
ORAL HEALTH IN PAST POPULATIONS: CONTEXT, CONCEPTS AND CONTROVERSIES

Cohen and Crane-Kramer (2007)

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better characterized at the origin and the ecological and cultural costs, that is, the energy and stress, relative work load of samples from diverse regions. Problems of small and large scale, the scale of chronology periods and the impact of this broadening of the sample was clear—that the relationship of diet and health. The decline in the frequency of dental caries continued. These findings confirms the role of diet, and the detrimental effects of diet and nutrition and on oral health.

Paleopathology at the fringe

Cohen and Crane-Kramer (2007) and their colleagues have provided an update and reassessment of the evidence for oral health and diet in the prehistoric record. A significant diversity of sites and regions (35.8% of the world's population, 70% of the world's population, and 65% of the world's population) were included in the analysis (2007). In these analyses, Thailand (two chapters) appeared most often, followed by Malaysia, Thailand (2), Indonesia, and China. Dental health, diet and disease (seven chapters; 81 percent), and the role of diet and nutrition in oral health and dental caries as a sequel, Ancient Health, due to an increase in the distinctiveness of regional variations including differences in ecology, culture (food preparation) and staple cultigen. Figure 22.4 in Ancient Health (Cohen and Crane-Kramer 2007:329) compares temporal trends in frequency of dental caries in all regions discussed. While caries were not reported for three areas (Bahrain, Mongolia, and South Africa), the majority—twelve regions—show a gradual or steep upward trend in caries frequencies, and two (England and UAE) show short-term variability with fluctuating increases and decreases in caries frequency. Thailand is represented by two studies. Despite archaeological evidence for increasing rice production from the Bronze Age (Ban Lum Khao) to the Iron Age (Noen U-Lok), tooth count and individual caries rates are very similar (Domett and Tayles 2007). Results from two additional sites in northeastern Thailand reveal contrasting trends, with caries frequency decreasing at Ban Chiang and increasing at Non Nok Tha (Douglas and Pietrusiewski 2007). Earlier indications suggested that the close relationship between oral health and agriculture found among native North Americans is not directly applicable to the southeast Asia context, where rice is the primary cultigen (Tayles et al. 2000). Several contributors to the Bioarchaeology of Southeast Asia (Ostenhjem and Tayles 2006), found little support for the predicted decline in oral health and rise in caries frequency with the origin and intensification of rice agriculture. The increased emphasis on Asian sites and samples in Ancient Health confirms that caries should not be interpreted unequivocally as an index of farming in all regions or for all cultigens. A summary of changing perspectives on rice cultivation and caries frequencies in the decade since the initial study by Tayles and colleagues (2000), asks “Can dental caries be interpreted as evidence of farming?: The Asian experience.” (Tayles et al. 2009). The important lesson here is that the current understanding of disease—subsistence and diet relationships are dependent on the geographic, cultural, ecological and temporal context of samples comprising the database. Furthermore, generalizations are likely to be inaccurate or wrong without critical consideration of all variables, and the advancement of research will require periodic reassessment of consensus opinion, especially when analyzing new samples from poorly documented regions.

Two concerns regarding research on diet and dental pathology that should be important themes for future investigation are: a) closer examination of hypothesized differences in dental pathology profile between coastal and inland groups, and b) more attention to changes in frequency of enamel hypoplasia with agriculture and related mortality effects. Several contributions to Ancient Health reported on dental health of coastal samples, from Bahrain, the southeastern U.S., Peru, and the United Arab Emirates, others examined inland and coastal samples from the same region Florida, Georgia, and North Carolina with some consistent and some divergent results depending on lesion considered, sample size and local ecological variables.

Building on previous research by Turner (1979) on Jomon health and subsistence, and using the concept of dental pathology profile (Lukacs 1989), a new and potentially valuable study constructed a theoretical dental pathology profile for marine-dependent groups (Selwood 2010). After identifying groups with marine-dependent diets using stable isotopes, a suite of pathological dental lesions associated with marine dependent diets was established and labeled the marine-dependent dental pathology profile (MDDPP). This pathology profile included a combination of low-frequency (abscesses, antemortem tooth loss and caries) and high-frequency (calculus, periodontal
disease, and severe wear) conditions. Despite omnipresent obstacles such as disparities in sample size, some small or fragmentary samples, and limitations relating to differences in method of reporting frequencies of pathological lesions, the idea of refining and narrowing the applicability of dental pathology profile to more specific dietary regimens is promising. Though the use of stable isotopes in concert with data on dental pathology to more precisely reconstruct diet in past populations has an established history (Lubell and Jackes 1994; Keenleyside 2008), the field would benefit from more extensive and creative application of this combination of methods.

Enamel hypoplasia exhibits a less consistent trend than caries with the onset and intensification of agriculture, as evidenced by the papers in Ancient Health and summarized by Cohen and Crane-Kramer (2007:326, Fig. 22.1). Nevertheless, linear enamel hypoplasias are especially useful in reconstructing the chronological timing of stress events during growth and development, because the age at which a defect formed can be estimated from its position on the labial surface of the tooth crown. The most reliable method of estimating the time of defect formation, and therefore the age at which a stress event occurred, remains controversial (Reid and Dean 2000; Martin et al. 2008; Ritzman et al. 2008). Nevertheless, bioarchaeological analysis of hypoplastic enamel is said to be an “untapped” source of valuable information that now provides tentative support for a concept known as the Barker Hypothesis, also more fully described as the Developmental Origins of Health and Disease Hypothesis (DOHaD) (Armelagos et al. 2009). Currently only a handful of studies support the contention that physiological disruptions in growth and development that occur in utero or in early childhood (indicated by enamel hypoplasia) are associated with increased morbidity later in life and with early mortality in adolescence or early adulthood. These linkages between developmental stress, as inferred from the presence and frequency of enamel hypoplasia, should be analyzed in relationship to early mortality in skeletal samples of foragers and farmers.

Caries etiology: new insights, complex etiology
This section is dedicated to new developments in understanding the etiology of a single, yet important dental disease: caries (WHO–ICD category K02). The relationship between diet, subsistence and dental disease has progressed over time through the research stages of plausibility, methodology and application (see above). The nature and extent of this relationship continues to be a major research initiative, in part because dental caries is a prevalent and costly public health concern (Vicira et al. 2008). Dental caries is a disease process involving progressive, focal demineralization of dental hard tissues by organic acids derived from bacterial fermentation of dietary carbohydrates, especially refined sugars (Featherstone 1987, 2000). Research developments in allied fields are continually and rapidly adding to knowledge regarding the multifactorial and complex etiology of dental caries. It is essential that anthropologists actively involved in reconstructing diet from dental pathology keep abreast of developments in clinical and genetic research that continue to broaden the range of etiological factors and influence the expression and frequency of dental caries. Advances on several fronts are helping clarify the mechanisms underlying cariogenesis and improving our understanding of sex differences in oral health. These include: a) variation in genes influencing enamel formation, b) genetic determinants of oral ecology, and c) genomic diversity of oral bacteria.
ORAL HEALTH IN FAST POPULATIONS: CONTEXT, CONCEPTS AND CONTROVERSIES

Genome-wide scans detecting associations between gene variants (quantitative trait loci) and every conceivable aspect of human variation have recently flourished and the number of publications is expected to peak in 2010 (Miller 2009). Not surprisingly, dental caries is among the diseases included in genome-wide association studies (GWAS). However, contrary to Miller’s pessimistic disappointment in the accomplishments of GWAS research, the findings and implications for caries research hold promise. The first such study of 46 families from the Philippines found caries suggestive loci for genes influencing saliva flow and diet preferences (Vieira et al. 2008). The study documents a significant sex difference in mean number of decayed, missing, and filled teeth (DMFT) between fathers (10.96) and mothers (14.45) in the Philippine families sampled. A protective locus for caries was identified on the X chromosome (Xq27.1) and has implications for the global and widely reported sex differences in caries experience (Lukacs and Largesaapla 2006; Lukacs and Thompson 2008). Subsequent studies of variation in selected candidate genes involved in amelogenesis have focused on ameloblastin, amelogenin, enamelin, tuftelin-I, and tuftelin-interacting protein 11, in a Guatemalan-Mayan sample (Deelely et al. 2008) and in a sample of Turkish children (Pati et al. 2008). Collectively, these studies suggest that variation in gene loci controlling enamel formation, especially ameloblastin, amelogenin, and tuftelin, contribute to observed differences in caries susceptibility. The authors hypothesize that variation in these gene loci contributes to microstructural alterations in enamel that may result in higher mineral loss under acidic conditions and may facilitate bacterial attachment to biofilms (Pati et al. 2008). This observation is especially interesting in view of Rose and Burke’s (2006) repeated references to early studies in the Classificatory / Descriptive (1840–1914) and Classificatory / Historical (1914–1940) periods concluding that increasing rates of dental decay (dental caries) in “civilized groups” might result from imperfect enamel or a decline in the quality of enamel. In the Contextual / Functional period (1940–1960), “The notion that a decline in the quality of enamel was the cause of the modern epidemic of dental disease was finally laid to rest.” (Rose and Burke 2006: 337). This transformation of an idea, from early broad explanatory statements regarding the diachronic decline in quality of enamel and rise of caries frequency, to a modern population and molecular genetic understanding is enlightening and informative. Current research suggests that enamel microstructure is influenced by genetic factors and is variable within and between populations and sexes resulting in differential susceptibility to caries. This important advance in knowledge of caries etiology has direct implications for researchers seeking associations between dental caries frequencies and diet in past populations.

Recent advances in genomic research have dramatically improved our view of caries microbiology by revealing the genome sequences of 15 different oral bacteria (Russell 2008). Understanding the genomics of plaque bacteria permits valuable insights into their evolution, physiology and regulatory mechanisms, some of which may be linked to virulence. Preliminary analyses of global diversity in the human salivary biome (Nasidze et al. 2009), coupled with advances in the ecology and succession of plaque microbial biofilms help elucidate proximate mechanisms involved in individual and sex differentials in caries susceptibility (Kolenbrander and Palmer 2004; Marsh 2004).
subsistence systems (Larsen 1983, 1998; Walker and Erlanson 1986; Lukacs 1996; Lukacs and Thompson 2008). Clinical research reveals a similar and consistent sex differential in oral health, especially in caries experience in diverse global samples of living populations (Haugejorden 1996; Lukacs 2008). The role that female sex hormones, pregnancy, and women’s reproductive history play in contributing to the sex difference in oral health is supported by clinical research, but often unappreciated by anthropologists (Lukacs and Largaespada 2006). An analysis of sex differences in dental caries prevalence in Hungary and India, and among the hunting and foraging Xavante adds to the database in support of the patterning of dental caries by sex (Lukacs in press). A growing appreciation for the sex difference in oral health and the importance of women’s reproductive history (total fertility) in contributing to differences in caries and tooth loss is encouraging (Arantes et al. 2009; Fields et al. 2009; Watson et al. 2010). The multifactorial and complex etiology of dental caries complicates analyses of the association between caries experience and parity (parity). Consequently, contradictory and conflicting reports reveal a nearly equal balance of early studies in support and against a causal linkage (see early sources in Mangi 1954). However, recently published results of age-controlled samples of pregnant and nonpregnant women in Chang Mai, Thailand found significantly higher caries frequency among pregnant women (Rakchanok et al. 2010; and sources cited therein). Indirect evidence in support of a relationship between caries experience and parity comes from the widespread pattern in which the sex difference in caries and tooth loss increases with age, especially during women’s reproductive years. Seeking evidence of a causal relationship between parity and poorer oral health in women will require greater care in research design that incorporates and controls for the diverse array of confounding variables, such as related oral lesions (periodontal disease and tooth-loss), the details of women’s reproductive histories, and contributing social and economic variables (Russell et al. 2010). A recent meta-analysis of gender differences in caries prevalence and experience in South Asia revealed significantly higher caries in girls associated with the onset of puberty (Lukacs 2011). Preliminary results of this meta-analysis of the sex disparity in dental caries in India exhibit the complex nature of confounding social and religious variables. These include son preference (daughter neglect) in health care and feeding regimens (Miller 1981), the popularity of fasting as religious practice among Hindu women (Pearson 1996), and the belief that dietary restriction during pregnancy is desirable because it will result in a less difficult birth (Vallianatos 2006). These beliefs and behaviors take on added significance when coupled with clinical evidence that fasting, undernutrition and malnutrition result in changes in oral ecology promoting caries and in increased caries rates (Alvarez 1995; Johansson et al. 1984; Poster et al. 2005, 2008). While social and religious factors such as these contribute to observed sex differences in caries experience, they are secondary to the synergistic impact of sex differences in diet and the influence of hormones and other systemic changes associated with pregnancy.

In sum, the results of genome-wide association studies hold promise for illuminating the causal mechanisms and pathways through which sex differences may in part originate. A significant outcome of the genetic research is that the sex difference in caries experience may be caused by: a) variation in the quality of tooth enamel (genes controlling enamel formation), b) variation in oral ecology (saliva flow and composition), c) variation in dietary preferences (olfaction and gustatory senses), and d) variation in the pathogenic microorganisms of the oral cavity. Clinical and
epidemiological research into the sex differential in oral health needs to accommodate and control for as many contributing variables as possible. It is encouraging to see that fertility and women’s reproductive biology are now being considered in the analysis of oral health of contemporary hunter gatherers (Arantes et al. 2009) and when sex differences are encountered in skeletal samples both female reproductive biology and sex differences in dietary behavior are considered (Klaus and Tam 2010; Temple and Larsen 2007). Future research into the sex bias in oral health holds promise for refining our understanding of the relative importance of key variables that contribute to it (genes, physiology, pregnancy, and culture).

Developmental dental anomalies: anthropological insights

This section focuses on the anthropological importance of documenting developmental dental anomalies (WHO-ICD categories K00-01, K07, K09 and K10) in past populations and emphasizes the value of clinical research to anthropological inference. The earliest descriptive accounts of dental pathology among Egyptians included attention to specimens with supernumerary teeth (fourth molars) and deficiencies in tooth number (third molar agenesis) (Ruffier 1920). Unerupted maxillary canine teeth (also known as suppressed or embedded) were noted in five male (2.98 percent) and two female (2.47 percent) adult skulls arising from an early analysis of the osteology of the Guanches, ancient inhabitants of Tenerife in the Canary Islands (Hooten 1925). Brief attention to dental occlusion, tooth rotation, impaction, and congenital absence was included in Nelson’s (1938) analysis of the Pecos Pueblo dentition. These early descriptions of developmental dental anomalies do not discuss causal factors or hypothesize etiology. An early survey of congenital absence of teeth cites examples from fossil hominids, as well as prehistoric and living humans (Brothwell et al. 1963). Importantly, Brothwell and colleagues suggest potential factors contributing to the observed patterns of congenital absence, including evolutionary and genetic mechanisms such as natural selection, genetic drift, and inbreeding in isolated populations.

Relative to studies of diet and dental disease, the documentation and analysis of developmental anomalies may be less common simply because: a) the traits under investigation (hypodontia, supernumerary teeth, tooth displacement and rotation) occur in low frequency, and therefore large sample sizes are required for analysis, and b) dentitions recovered from archaeological contexts are often affected by postburial diagenesis and are either fragmentary, incomplete or distorted. Nevertheless, study of dental anomalies in prehistoric samples provides valuable insight into diverse aspects of early population dynamics and evolution. One benefit of documenting dental anomalies in past populations is better understanding the nature and origin of these afflictions. This approach relies on evidence that many dental anomalies of shape, form, number and position have a significant genetic component. Representative examples of the kinds of pathological dental anomalies that have been documented in the course of bioarchaeological research and their relevance to paleopathology are briefly summarized.

The frequency and etiology of a developmental anomaly of tooth position, known as canine-premolar transposition (Mx.C.P1) has been described among living samples in India (Chattopadhyay and Srinivas 1996) and North America (Pec 1993; Pec and Pec 1995). Variation in trait frequency ranges from a low of 0.12–0.13 percent among Asian Indian and Saudi Arabian samples (respectively), to a high of
8.49 percent among native Americans from Santa Cruz Island, California. The high trait frequency among Santa Cruz Islanders has been interpreted to result from an inbreeding effect due to population isolation (Nelson 1992). Individual cases of canine-premolar transposition occur in Bronze Age and Iron Age samples from South Asia (Lukacs 1998) and the trait is present in low frequency (1.8 percent; 9 of 500) in the Pecos Pueblo sample from New Mexico (Burnett and Weets 2001).

Developmental dental anomalies commonly observed in prehistoric and living samples include reduction in size, displacement (or axial rotation) and congenital absence of teeth. Two classes of teeth have received special attention with regard to prevalence of rotation, displacement, or agenesis: maxillary lateral incisors and third molars (Garn et al. 1963). These teeth frequently exhibit significant variation in size and demonstrate a predisposition to dental reduction referred to as "peg-shaped" incisors or "barrel-shaped" molars (Montagu 1940; Le Bot and Salmon 1977; Le Bot et al. 1980). Permanent dental agenesis in modern humans is most frequent in third molars, followed by lateral incisors and second premolars (Polder et al. 2004). The high frequency of missing lateral incisors in an Iron Age sample from Noen U-Loke (Thailand) was cautiously attributed to agenesis, rather than pathological loss or ritual ablation (Nelsen et al. 2001). The authors infer that endogamy, possibly due to isolation, may have contributed to the high prevalence (79 percent of adults; 30 of 38) of individuals with at least one missing incisor in either the maxilla or mandible in this sample.

In a clinical sample of 1620 subjects, Baccetti (1998) found a significant association between dental agenesis (aplasia) and tooth-rotation anomalies. Maxillary lateral incisor agenesis was significantly associated with premolar rotation, and the reverse relationship, P4 agenesis in association with P2 rotation, was also significant (Baccetti 1998). This association of dental anomalies has been documented in a prehistoric specimen from Tuscany. Two independent studies describe the association of developmental anomalies in an Etruscan adolescent from the 6th century B.C. (Baccetti and Moggi-Cecchi 1995; Kocsis et al. 1995). Agenesis of second maxillary premolar teeth in this individual is associated with maxillary lateral incisors that are reduced in size and have a 'peg-shaped' form.

In addition to its presence in fossil hominin taxa Homo erectus (Dmanisi D2700; Rightmire et al. 2006) and H. floresiensis (LB 1), axial rotation of maxillary P4s has been observed among living and Neolithic South Asians (see Figure 50.3), prehistoric Guanches of the Canary Islands (Lukacs et al. no date), and Rampasasa pygmies from Flores (Jacob 2006:13424). Clinical evidence supports a genetic influence on the expression of UP4 agenesis and rotation and an association between it and the absence or diminution of UI2 and UM3. Appreciation of an interpretative model that regards intertrait associations as complex, interdependent, and genetic in origin (Baccetti 1998; Kotsonitis et al. 1996), can add significantly to the understanding of past populations structure. However, palaeopathologists must exercise vigilance in observing and recording dental agenesis, axial rotation and tooth size reduction at multiple loci in the dental arcade (I, P, M). These attributes—axial rotation, reduced or absent maxillary lateral incisors and third molars—are more frequent in females and exhibit increased frequencies in genetic isolates where inbreeding and/or founder effect can increase expression of rare genetically influenced conditions. Consequently, systematic observation of these developmental genetic anomalies should be included in dental pathology research protocols, for the insights they provide regarding prehistoric population dynamics.
CONCLUSION

The field of dental paleopathology consists of two primary research foci. One documents the prevalence and distribution of dental diseases in past populations to better understand the history of oral health in relation to cultural changes in behavior, especially diet and subsistence. The other investigates the frequency of developmental dental anomalies in fossil hominins and prehistoric skeletal samples for insights into evolutionary and genetic mechanisms influencing dental variation.

The field of dental paleopathology is broadly interdisciplinary and relies on developments in evolutionary theory and genetics, as well as advances in epidemiology and the clinical study of dental diseases and anomalies. In historical perspective, the field continues to be concerned with some of the same issues and research questions that intrigued early researchers interested in oral health and dental anomalies. This survey of dental paleopathology focuses on four specific topics:

1) Examples of a wide range of dental diseases and anomalies in pre-Holocene hominins illustrates the great antiquity of afflictions that also occur in modern humans (caries, supernumerary teeth, enamel hypoplasia and periodontal disease, for example). While some examples represent single unique occurrences, others such as the analysis of linear enamel hypoplasia is based on adequate samples that allow insight on the relative level of developmental stress in early hominins (Australopithecus vs. Paranthropus) and in later premodern hominins (Neandertals vs. modern humans).

2) An assessment of the current status of research on diet, subsistence and dental disease confirmed the general pattern of declining oral health on the adoption and intensification of agriculture. However, rice-dependent societies of Southeast Asia appear to be an exception to this pattern and demonstrate that generalizations regarding subsistence and oral health from one geographical region (native North America) may not be applied universally.

3) Recent advances in understanding of caries etiology have yielded new insights from research in genetics (genome wide scans), clinical dentistry and epidemiology. Variation in enamel protein gene loci may result in altered enamel microstructure, influencing plaque adherence and rate of demineralization, thereby contributing to variation in cariogenesis. Pregnancy and malnutrition have a multifactorial, yet often unappreciated, impact on caries development. For example, both pregnancy and malnutrition have been documented to influence saliva flow rate and composition, key components in the etiology of dental caries that may contribute to the observed differential prevalence of caries by sex and by nutritional status.

4) Developmental and genetic dental anomalies have had an important place in dental paleopathology from the earliest pioneering research on ancient Egyptians. Today better understanding of the genetics underlying dental agenesis, tooth size reduction, and axial rotation of teeth allows for more precise inferences regarding the role of evolutionary forces on the expression and frequency developmental dental anomalies.

If this survey generates new questions and stimulates creative and innovative research resulting in further advancement of the field of dental paleopathology, it will have been a successful endeavor.
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