Advances in Human Palaeopathology

Edited by

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To Hattie and Maralyn
Simon Mays

To Rita
Ron Pinhasi

Contents

Preface

Traditionally, in palaeopathology the principal emphasis was on descriptions of individual cases, principally in order to demonstrate the diagnosis of specific conditions and to help establish the antiquity of various diseases. In recent decades, however, although the case study still has a place, there has been a greater emphasis on population studies. In part, this reflects a move away from a medico-historical orientation to one where addressing archaeological questions takes precedence. A dominant theme is now evaluating disease frequencies at a population level and integrating this with cultural data pertaining to the populations under study from archaeological (or historical) sources in order to address questions of broader archaeological interest.

Several factors underpin this approach in palaeopathology, among which are the following.

1. An understanding of biases and limitations of the skeletal record caused by differential skeletal survival and other factors.
2. Rigorous quantification of disease or lesion frequency in fragmentary and incomplete remains.
3. The accurate ascription of causation to bony pathologies (be it diagnosis of specific disorders or ascription of more general causes to non-specific lesions, such as dental enamel hypoplasias).

As regards the first of these, our understanding of factors affecting skeletal decomposition in the burial environment and the mechanisms of diagenesis has been greatly increased in the last 15 years by the application of physical, chemical and microscopic analyses to ancient bone. As regards the second point, we are increasingly coming to grips with the problems of quantifying lesions and diseases in incomplete and fragmentary skeletons, and the potential of applying epidemiological methodologies to ancient remains has begun to be appreciated. There is also an increasing realization that we may need to go beyond recording of simple prevalence rates in order to unlock more fully the information on earlier human populations contained in skeletal pathology. More workers are now attempting to record differences in severity of lesions objectively, and it is becoming increasingly common for workers to record whether lesions were active or healed at time of death. As regards the third point, the increasing use of medical imaging techniques, microscopic examination of lesions and biomolecular analyses has been a major aid to the description and/or diagnosis of disease in human remains. In addition, more workers are integrating the study of specific or non-specific disease with aspects such as growth and are examining associations between the occurrence of different types of lesion or disease. These studies aid the interpretation of skeletal disease. It was in the light of these developments that we conceived the current volume.

We made the decision to concentrate mainly (but not exclusively) on skeletal remains rather than preserved soft tissue. This is simply because in most instances the skeleton is all that survives. We have organized this volume into two parts. Part 1 deals with analytical issues in palaeopathology. The first contribution, by Gordon Turner-Walker, deals with the diagenesis of buried skeletal tissues. He describes the changes wrought by chemical and microbial agents in the organic and inorganic components of skeletal tissues. He considers some of the determinants of the rate of diagenesis; chief among these is the availability of water in the burial environment, together with its pH and the presence or otherwise of dissolved ionic species. As Turner-Walker points out, a sound understanding of post-depositional changes to hard tissues is essential when attempting to interpret pathological conditions in skeletons. Developing this theme in Chapter 2, Pinhasi and Bourbou discuss how skeletal survival, as well as other factors such as excavation methods and ancient burial practices, may bias a skeletal sample and, hence, complicate the interpretation of disease at a population level. They also emphasize the importance of controlling for age at death in population studies in palaeopathology and provide a case study to illustrate one approach to this.

The third contribution, by Pinhasi and Turner, discusses some analytical approaches to the quantitative study of disease frequency in palaeopopulations: palaeoepidemiology. They discuss key paleoepidemiological concepts and provide hypothetical examples to illustrate the application of some of these concepts to skeletal data.

Chapters 4–8 focus on techniques for examining pathological changes in ancient human remains. Anne Grauer discusses macroscopic data collection in skeletal palaeopathology in Chapter 4. She notes that, despite the advent of technologically advanced techniques, gross visual examination of specimens remains the foundation of palaeopathological investigation. She discusses the historical background of study and evaluates attempts toward standardizing terminology and data collection. She identifies a number of problems and issues germane to this area, and offers suggestions as to how these might be resolved.

The next four chapters concentrate on the application of medical imaging and histological and biomolecular techniques in palaeopathology. Radiography is the oldest and still the most frequently used augment to visual examination of specimens in palaeopathology. In Chapter 5, Simon Mays discusses plain-film radiography, quantitation of cortical bone thickness from radiographs (radiogrammetry) and various radiological methods of measuring bone density. The principles of these techniques are explained and their contribution to palaeopathological description and diagnosis discussed. In Chapter 6, Lynnerup discusses the imaging by CT of hard and soft tissues in mummies and bog-bodies. An important focus of both Mays' and Lynnerup's contributions is on the issues raised and problems encountered when applying imaging techniques developed for medical application to ancient human remains.

Turner-Walker and Mays discuss the microscopic study of disease in skeletal remains in Chapter 7. Focusing principally on light and electron microscopy, they discuss sample preparation techniques, the effects of diagenesis on the histological appearance of buried bone and the role of microscopic studies of skeletal lesions in palaeopathology. Histological structures may be studied in a qualitative manner and any abnormalities noted may assist in diagnosis of disease. They may also be studied quantitatively (histomorphometry) to investigate the extent of progressive metabolic conditions such as osteoporosis or to estimate age at death. The contribution concludes with a discussion of the potential role of newer microscopic techniques.

Donoghue covers the fast-moving field of biomolecular study of ancient infectious disease in Chapter 8. Focusing principally on the study of DNA, the degradation and authentication of ancient DNA are discussed and the contribution of biomolecular study to the palaeopathology of various specific infections is evaluated. The potentially important contribution to be made by ancient DNA studies to our understanding of the evolution of disease-causing microorganisms is also considered.

The systematic gathering of large amounts of osteological data raises questions of how best to organize these data and make them available to the wider scholastic community. In the last chapter in this section, Bill White reviews issues concerned with the establishment and maintenance of computerized databases of human remains. He identifies several different types of database, ranging from simple inventories to help researchers locate archived collections, to those which include considerable osteological detail with the intent that scholars use the data directly in their research. He presents an evaluation of the strengths and weaknesses of some of the major extant databases of human remains, and discusses possible future directions.

In Part 2 we concentrate on the diagnosis and interpretation of various classes of disease. We have not attempted to be comprehensive in our coverage of the different categories of disease, but rather have endeavoured to select those where recent advances have made themselves most felt.

Don Ortner discusses diagnostic issues in the evaluation of skeletal infectious disease in Chapter 10, with an emphasis on macroscopic study. He reviews the major infectious diseases that can be identified on the skeleton and provides an extensive photographic illustration of lesions, and emphasizes the need for careful description of lesions and rigorous differential diagnosis.

In his chapter on metabolic bone disease, Simon Mays reviews the pathophysiology, palaeopathological diagnosis and interpretation of vitamin D deficiency, vitamin C deficiency, osteoporosis and Paget's disease of bone. Most studies of the former two conditions have been conducted in order to investigate biocultural questions concerning living conditions and diet. Palaeopopulation studies of the latter two have been mainly orientated toward increasing our understanding of the risk factors for these poorly understood conditions which continue to be important contributors to morbidity and mortality today.

A review of tumours and tumour like processes is provided by Don Brothwell in Chapter 12. He gives a wide-ranging review of the archaeological evidence for both benign and malignant tumours in hard and soft tissues, and considers the potential for relating changes in frequency through time to environmental or cultural factors. The need for collation of widely scattered data and for rigorous statistical analysis is emphasized.

In his chapter on dental disease, Alan Ogden concentrates on some key recent developments in our understanding. He describes a new type of dental enamel hypoplasia, discusses diagnostic criteria for periodontal disease and presents a simple scoring system. He then proceeds to discuss the categorization and significance of periapical voids in alveolar bone.

Pia Bennike discusses trauma in skeletal remains in Chapter 13. She outlines various fracture types and their recognition and quantification in skeletal populations. She also considers the significance of decapitation and mass graves. To illustrate her points, she draws particularly on examples from Denmark and other parts of Scandinavia.

In her chapter on congenital anomalies, Ethne Barnes gives an account of the morphogenesis of different areas of the skeleton and the anomalies which arise from disturbances to that process. Because genetic factors are important causes of most of the anomalies discussed,

their biocultural significance lies chiefly with what they can reveal of relationships between populations and between individuals. She illustrates this last point with examples from the palaeopathological literature.

In the final contribution, Pinhasi discusses the value of growth studies of past populations. He considers some of the methodological issues pivotal to such studies. He emphasizes the value of the study of multiple skeletal elements in order to provide a fuller picture of bone growth, and of the potential of studies that attempt to ascertain the effect of disease on growth in past populations. He illustrates these points with reference to key palaeopathological publications.

Although each contribution reflects the author or authors' own unique perspective, a number of common themes do seem to emerge. The quantification of lesions and disease frequency in archaeological skeletal remains continues to present challenges. The benefits of collating data generated by different authors are clear; but, in reality, it is often difficult to compare data between publications, not least because of the sometimes rapid developments and advances in recording methodologies and diagnostic criteria. Gross study of skeletal lesions is likely to remain the foundation of palaeopathology, and there is a continued emphasis on the development and refinement of macroscopic diagnostic criteria. However, although diagenesis complicates the interpretation of medical imaging and histological and biomolecular analyses of ancient human remains, these techniques are likely to play an increasing role in future. The increasing use of technologically advanced laboratory techniques, together with the increased appreciation of the value of analytical models from other disciplines such as epidemiology, and the need to integrate palaeopathological data with historical and or archaeological data, means that collaboration with other disciplines is more vital than ever for the continued development of palaeopathology as a field of study.

Simon Mays and Ron Pinhasi

Contributors

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Ethne Barnes is a physical anthropologist and palaeopathologist consultant and independent researcher, based in Tucson, Arizona. She is recognized for establishing the morphogenetic approach to analysing developmental defects of the skeleton in palaeopathology. She holds a PhD in physical anthropology from Arizona State University (1991), an MA in anthropology (1977) and BSN (1974) from Wichita State University. She has former clinical and teaching experiences prior to becoming consultant to the Corinth Excavations of the American School of Classical Studies at Athens in 1994, and with INAH excavations in Sonora, NW Mexico, in 1998. Research and consultations also include archaeological projects in other parts of Greece, Turkey, China, South America and North America. Major publications include *Developmental Defects of the Axial Skeleton in Paleopathology* (University of Colorado Press, 1994) and *Diseases and Human Evolution* (University of New Mexico Press, 2005).

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Pia Bennike received her PhD from the University of Copenhagen, Denmark, in 1984. She is currently associated Professor at the Laboratory of Biological Anthropology, Department of Forensic Medicine, University of Copenhagen. She is teaching skeletal biology for archaeologists and palaeopathology (PhD courses, and EAA Summer School), and is supervisor for a number of medical and archaeological students. Her research encompasses most areas of human osteoarchaeology and especially palaeopathology. Key publications include: *Palaeopathology of Danish Skeletons* (Akademisk Forlag, 1985); 'Ancient trepanations and differential diagnosis' in *Trepanation: History, Discovery, Theory*, Arnott R, Finger S, Smith CUM (eds) (Routledge, 2003); 'Rebellion, Combat, and massacre: a medieval mass grave at Sandbjerg near Næstved' in *Warfare and Society: Archaeological and Social Anthropological Perspectives*, Otto T, Thrane H, Vandkilde H (eds) (Aarhus Universitetsforlag 2006); and various publications in Danish.

She is currently vice-president of the European Anthropological Association (former president 2000–2004) and president elect of the Paleopathology Association.

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Dr Chryssi Bourbou is a Research Associate at the 28th Ephorate of Byzantine Antiquities (Hellenic Ministry of Culture). Her main research interests focus on the bioarchaeology of

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Don Brothwell is now emeritus professor of human palaeoecology in the University of York. He has a doctorate from the University of Stockholm, has taught in the universities of Cambridge, London, and York, and for a period was Head of the Sub-Department of Anthropology (now extinct) in the British Museum of Natural History. He still teaches, and currently researches on fossil hominins and mammoths, recent *Microtus*, and the palaeopathology of humans and other mammals. Recent publications include a chapter in *The Myth of Syphilis: The Natural History of Treponematosis in North America*, Powell M, Cook D (eds) (University Press of Florida, 2005) and 'Skeletal atrophy and the problem of the differential diagnosis of conditions causing paralysis', *Anthropologia Portuguesa*, 2000. He is currently trying to find time to return to his first love, art (being originally an art school dropout).

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Helen Donoghue received her PhD from the University of Bristol. She spent 6 years at the MRC Dental Unit in Bristol, investigating oral microflora. For 4 years she was Lecturer in Medical Microbiology at the University of Bradford and is now Senior Lecturer at University College London. Her recent research has focused on DNA from pathogenic microorganisms in archaeological material, using PCR. Most work has been done on ancient tuberculosis, leprosy and, more recently, parasites such as schistosoma and leishmania. Key publications include: 'Widespread occurrence of *Mycobacterium tuberculosis* DNA from 18th–19th century Hungarians' (with Fletcher, Holton, Pap and Spigelman), *American Journal of Physical Anthropology*, 2003; 'Molecular analysis of *Mycobacterium tuberculosis* from a family of 18th century Hungarians' (with Fletcher, Taylor, Van Der Zanden, and Spigelman), *Microbiology*, 2003; and 'Co-infection of *Mycobacterium tuberculosis* and *Mycobacterium leprae* in human archaeological samples – a possible explanation for the historical decline of leprosy' (with Marcsik, Matheson, Vernon, Nuorala, Molto, Greenblatt, and Spigelman), *Proceedings of the Royal Society of London, Series B*, 2005. She is a Fellow of the Royal Society for Tropical Medicine and Hygiene, a member of numerous microbiological societies and of the Paleopathology Association.

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Anne Grauer received her PhD from the University of Massachusetts–Amherst in 1989. She is currently a Professor in the Department of Anthropology at Loyola University of Chicago. Her research focuses on exploring issues of health and disease in medieval England and within non-Native American groups in the USA. Of particular interest is the use of documentary evidence, combined with skeletal analyses, to understand the lives of women. In 1993, she was awarded the National Science Foundation Presidential Faculty Fellowship to support her incorporation of undergraduate students into scientific research. Key publications include: *Bodies of Evidence: Reconstructing History Through Skeletal Analysis* (editor, Wiley-Liss, 1995); *Sex and Gender in Paleopathological Perspective* (co-editor Stuart-Macadam, Cambridge University Press, 1999); 'Where were the women?' in *Human Biologists in the Archives*, Herring DA, Swedlund AC (eds) (Cambridge University Press, 2003). She has recently served on the editorial board of the *American Journal of Physical Anthropology*, the Executive Board of the American Association of Physical Anthropologists, and as Treasurer and Webmaster of the Paleopathology Association.

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Journal of Physical Anthropology, 2001; 'Skeletal manifestations of rickets in infants and young children in an historic population from England' (with Brickley and Ives), *American Journal of Physical Anthropology*, 2006. He is a member of the managing committee of the British Association for Biological Anthropology and Osteoarchaeology (BABAO), of the Human Remains Advisory Panel of the UK Governmental Department of Culture, Media and Sport, and is Secretary of the Advisory Panel on the Archaeology of Christian Burials in England.

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Alan Ogden was trained as a dental surgeon, and was a Lecturer/Associate Specialist in Restorative Dentistry at Leeds Dental Institute for 20 years, with an especial interest in implants, and in 1988 was awarded his doctorate. He then trained in osteology and palaeopathology at Bradford and has been a Research Fellow/Contract Osteologist in the Bioanthropology Research Centre at the University of Bradford since 2001. He has run the postgraduate courses on musculo-skeletal anatomy in 2003 and archaeology of human remains in 2004 and regularly lectures on the anatomy and palaeopathology of teeth and jaws. He has produced skeletal reports on more than 2000 medieval individuals from Norton Priory, Chichester Leper Hospital and Hereford. He has reported on 60 middle Bronze Age burials from a British Museum dig in the Lebanon, and he is currently re-examining 50 Neolithic individuals excavated in the 1860s from barrows in the Yorkshire Wolds. Recent joint publications include 'Tallow Hill Cemetery, Worcester: the importance of detailed study of post-mediaeval graveyards' and 'A study of Paget's disease at Norton Priory, Cheshire, England' *British Archaeological Reports* International Series 2005; 'Morbidity, rickets, and long-bone growth in post-medieval Britain', *Annals of Human Biology*, 2006; 'Gross enamel hypoplasia in subadults from a 16th–18th Century London graveyard', *American Journal of Physical Anthropology* (in press). A former Curator and Honorary Member of the British Society for the Study of Prosthetic Dentistry, he is a member of the American Association of Physical Anthropologists, the Paleopathology Association and the British Association for Biological Anthropology and Osteoarchaeology.

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Gordon Turner-Walker was awarded a PhD by the University of Durham, England, in 1993. He worked as the archaeological conservator for Norfolk Museums Service before taking up a 3-year postdoctoral fellowship at the Norwegian University of Science and Technology investigating osteoporosis in the medieval population of Trondheim. He is currently Associate Professor of cultural heritage conservation at National Yunlin University of Science and Technology, Taiwan. His main areas of research are post-mortem alterations to bone chemistry and microstructure, the archaeology of osteoporosis and the degradation of cultural materials in marine and terrestrial environments. Key publications include: 'The West Runton fossil elephant: a pre-conservation evaluation of its condition and burial environment' *The Conservator*, 1998; 'Quantifying histological changes in archaeological bones using BSE-SEM image analysis' (with Syversen), *Archaeometry*, 2002; 'Sub-micron spongiform porosity is the major ultra-structural alteration occurring in archaeological bone' (with Nielsen-Marsh, Syversen, Kars and Collins), *International Journal of Osteoarchaeology*, 2002; 'Osteoporosis in a population from medieval Norway' (with Mays and Syversen), *American Journal of Physical Anthropology*, 2006. He is a Fellow of the International Institute for Conservation of Historic and Artistic Works.

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PART 1

Analytical Approaches in Palaeopathology

1

The Chemical and Microbial Degradation of Bones and Teeth

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INTRODUCTION

The physical survival of bone is integral to any kind of palaeopathological study. Not only must the skeleton survive in the burial environment or tomb, it must retain sufficient strength to be excavated, lifted, archived and studied. When assessing skeletal remains for pathological conditions, it is also important to distinguish successfully between bone lesions that arose ante- or peri-mortem as a result of disease or trauma, and damage caused by post-mortem processes taking place in the burial environment. A sound understanding of post-mortem changes to mineralized tissues is, therefore, essential when attempting to interpret pathological conditions in skeletons, particularly those (the majority) that have been buried in soils for centuries or millennia. Unlike some gross post-mortem patterns of destruction caused by root action, insects or rodents, which are frequently visible on the outer surfaces of the specimens, microbial and chemical degradation is microscopic in nature and can influence the interiors of the bones as well as their surfaces. This unseen deterioration not only contributes to the fragility of archaeological bones, but by altering the chemistry and microstructure of the tissues it can also have a serious impact on chemical or radiological analyses and on the radiocarbon dating of skeletons (Lee-Thorpe and van der Merwe, 1987; van Klinken, 1999; Mays, 2000; Petchley and Higham, 2000; Dupras and Schwarcz, 2001). The potential for leaching and the movement of soluble salts into and from the bone structure also has a bearing on the interpretation of radiodensitometry (Mays, Chapter 5 this volume) and measurements of bone density using clinical techniques such as dual energy X-ray absorptiometry (Agarwal and Grynpas, 1996; Mays, 1999; Mays *et al.*, 2006). Thus, changes to skeletal tissues arising from their interaction with the burial

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environment and from the actions of soil microorganisms have an impact on almost all aspects of palaeopathological study and the value of human skeletons as a source of information about the past.

In recent decades, rapid developments in the field of biomolecular archaeology have demonstrated that physical and microscopic integrity is no longer enough when considering the research potential of an individual skeleton or assemblage. The integrity of any isotopic and molecular evidence contained within bone and tooth tissues is equally important (Muyzer *et al.*, 1992; Cattaneo *et al.*, 1995; Evershed *et al.*, 1995; Baron *et al.*, 1996; Taylor *et al.*, 1996; Weser *et al.*, 1996; Braun *et al.*, 1998; Stott *et al.*, 1999; Götherström *et al.*, 2002; Geigl, 2002). Recognition of this has driven much of the research into how and why skeletal tissues degrade in the soil, and the progress made in the understanding of these diagenetic processes during the last decade of the 20th century and early years of the 21st century has been almost as dramatic as the huge strides made in the analyses of DNA, lipid and protein residues over the same period.

Compared with other scientific studies of archaeological and fossil bones, the study of bone deterioration is relatively young. The term *taphonomy*, to describe post-mortem processes influencing bone survival, was introduced nearly 70 years ago by Efremov (1940), and these 'laws of burial' were invoked to help interpret fossil and archaeological bone assemblages. In its broadest sense, taphonomy concerns all aspects of the passage of organisms from the *biosphere* (the living world) to the *lithosphere* or Earth's crust (Olson, 1980). The primary goal of taphonomic studies is to work backwards from the surviving bone assemblages to the composition, structure and dynamics of the parent populations (human or animal) using evidence recovered from the bones themselves, the nature of their contexts and an understanding of post-mortem processes (Olsen, 1980). The geological term *diagenesis* is defined as the processes by which sediment is transformed into sedimentary rock under conditions of low temperature and pressure. In recent years, this term has been adopted to describe the changes undergone by skeletal tissues in the burial environment. These changes may involve dissolution of bone tissue or its cementation by exogenic minerals, recrystallization of bone mineral or its replacement by other mineral species. These alterations to bone tissue are often crudely referred to as fossilization (Behrensmeyer and Hill, 1980) and a combination of taphonomic and diagenetic processes determine whether a bone decays and ultimately disappears or persists throughout the course of archaeological or geological time.

As early as the middle years of the 19th century, microscopic examination of ancient bones had identified the potential importance of microorganisms in the destruction and degradation of bone tissues. In 1864, Wedl examined thin sections of ancient bones under the light microscope and described small channels or tunnels penetrating the bone tissues (Wedl, 1864). Roux, working in the late 19th century, also identified these features in fossil bones and termed them bored channels or *Bohrkanäle* (Roux, 1887). The presence of fine, brown filaments visible in these tunnels suggested to him the action of fungi in their formation. Thus, from the outset, the action of fungi was implicated as the principal causal factor in the destruction of dead bone tissues – an assumption that persisted for more than 100 years and remains contentious today.

By the middle of the 20th century, chemical analysis of ancient skeletal tissues was being used as a means of absolute dating, initially with the introduction of fluorine-content dating and later followed by the radiocarbon revolution in archaeology. One of the earlier successes for carbon-14 dating was the confirmation of the Piltdown find of an 'English ape-man' as a modern hoax (de Vries and Oakley, 1959). Suspicions had already been voiced after

the failure to find the significant levels of fluoride in the bones that would be expected for a find of geological age. As a result of these developments, together with the introduction of uranium-series dating, calcium-41 dating and amino acid racemization dating, scientists became increasingly aware of the importance of understanding changes in the structure and composition of bones and teeth. These problems were later underlined during attempts to isolate faint dietary signatures, in trace element concentrations or in stable isotope variations, from larger diagenetic chemical alterations.

Before discussing post-mortem changes to skeletal tissues it is necessary to take a closer look at the nature of bones and teeth.

THE CHEMISTRY, ULTRASTRUCTURE AND MICROSTRUCTURE OF SKELETAL TISSUES

Skeletal tissues have a very ancient ancestry in the evolutionary record. Work on a group of fossil elements called *conodonts* has confirmed that these tooth-like structures represent the grasping mouthparts of primitive marine animals resembling eels (Briggs, 1992). These tiny fossils, measuring between 0.2 and 2 mm in length, are composed of the calcium phosphate mineral carbonate fluorapatite, and investigations of their microstructure have shown that they bear many features in common with the hard tissues (such as calcified cartilage, bones and teeth) of more advanced vertebrates (Sansom *et al.*, 1992; Schultze, 1996). These discoveries push back the origin of bony tissues, and consequently our ultimate ancestors, to the late Cambrian period, over 500 million years ago.

The basic chemistry of the calcified tissues bone, antler and tooth dentine (including ivory) is fundamentally the same, although they differ in their mode of growth and microstructure. Tooth enamel is rather specialized and differs from the other calcified tissues in that it is more crystalline and has a negligible organic content. Since bone is by far the most common calcified tissue, it is perhaps appropriate to consider it first before outlining the ways in which other tissues differ from it.

Bone

Living bone consists of three major components: organic matter, principally proteins; mineral in the form of calcium phosphates; and water. Here, the inclusion of water as a major constituent may seem pedantic, but the water contents of buried bones and the sediments that surround them play as important a role in their future integrity over archaeological time-scales as the chemistry and availability of biological fluids do during life. The organic matter in dry bone accounts for approximately 22–23 % by weight (Turner-Walker, 1993) and 40 % by volume (Nielsen-Marsh and Hedges, 2000a). About 90 % of this component is made up of long fibrils of Type I collagen that give living bones their tensile strength and a small degree of flexibility. Type I collagen molecules are highly organized, comprising three stretched helical amino acid chains which are themselves twisted into a triple helix. Collagen is characterized by a high glycine content, which makes up every third amino acid (33 %), with high levels of proline and hydroxyproline, which together account for a further 20 %. Each triplet is approximately 300 nm in length and 1.5 nm in diameter (Yamamoto *et al.*, 2000, De Cupere *et al.*, 2003).

The individual collagen molecules self-assemble or aggregate extracellularly and assume a hierarchical architecture with triplets organizing into bundles, called microfibrils, which ultimately form into fibrils and fibres. These fibre bundles align themselves with a quasi-hexagonal packing (Figure 1.1). Type I collagen is insoluble under normal physical and physiological conditions because of this well-ordered three-dimensional arrangement of the fibres, the ionic and hydrophobic interactions between adjacent amino acid chains, and a degree of cross-linking between the molecules. Strong aldehyde cross-links form between the lysine and hydroxylysine of adjacent collagen molecules and the microfibril is further stabilized by numerous intramolecular hydrogen bonds. Newly formed microfibrils are about 20 nm in diameter but grow in size with maturity up to approximately 90 nm, with an average microfibril diameter in young adults of 75 nm (Sarathchandra *et al.*, 1999). The unmineralized collagen network or organic matrix also contains non-collagenous proteins (including osteocalcin) and mucopolysaccharides which make up the remaining 10 % by weight (Tuross, 2003). Some of these non-collagenous proteins can be extremely stable over geological time-scales, strongly suggesting an intimate association with the mineral phase (Muyzer *et al.*, 1992; Smith *et al.*, 2005).

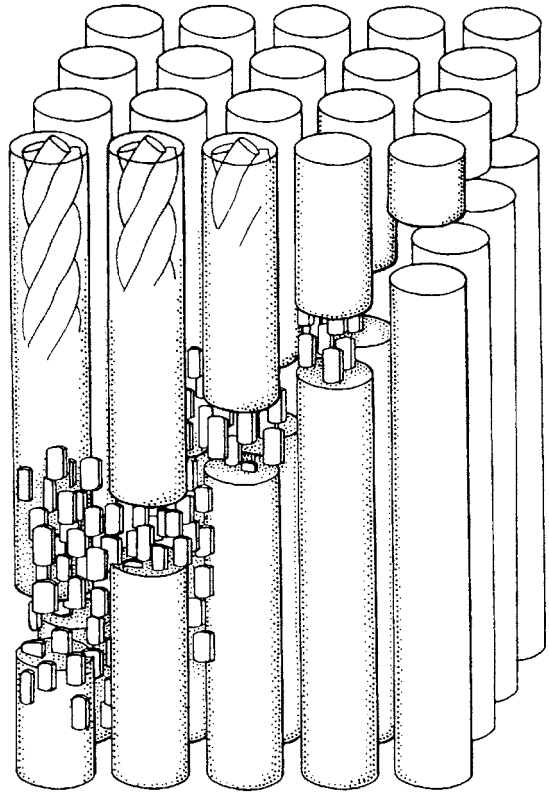

Figure 1.1 Diagrammatic representation of the close packing of collagen molecules (triplets) into fibrils. In reality the molecules are stabilized by intermolecular bonds. Progressive mineralization with small platelets of hydroxyapatite (HAP) proceeds in the gaps between the ends of the molecules and between adjacent triplets

The compressive strength of bone tissues is provided by the mineral component, which is generally accepted to be a stoichiometrically imperfect, carbonate-containing HAP analogue with a composition approximating to $Ca_{10}(PO_4)_6(OH)_2$, also called bioapatite. This mineral phase also includes traces of other anionic and cationic species that variously adsorb on crystal surfaces or substitute for Ca^{2+}, PO_4^{2-} and hydroxyl ions in the lattice. The exact nature of these mineral – ion interactions is not relevant to this discussion, but it is important to understand that they are closely related to the small sizes of the bioapatite crystals and their total available surface area. HAP crystals are plate-like in morphology and have currently accepted dimensions of approximately 35 nm by 5 nm and with a thickness of about 2–3 nm (Lowenstam and Weiner, 1989; Nielsen-Marsh *et al.*, 2000). It is widely recognized that the average sizes of the HAP crystals in bone increase with the maturity of the tissue. The extreme small sizes of the individual bone crystals, or more properly crystallites, present an enormous active surface area for bone mineral, estimated at between 100 and 200 $m^2\ g^{-1}$ (Posner, 1985; Newesely, 1989). It is unlikely, however, that this large active area is ever realized, because of the intimate association between the collagen matrix and the HAP. It has long been known that bone sections exhibit birefringence in polarized light, and this optical property arises from the orientation of both the collagen fibres and the HAP crystallites (Figure 1.2). These crystallites are embedded in the collagen matrix with their *c*-axes aligned parallel to the long axes of the fibres. These fibres are aligned in lamellae in which the fibre orientation in successive layers is rotated to give a plywood-like structure (Giraud-Guille, 1988; Weiner and Traub, 1992). Evidence points to initial deposition of HAP crystallites (primary mineralization) within gaps in the closely grouped collagen fibrils (Figure 1.1), with the bulk of the mineral load progressively filling the interfibrillar spaces (secondary mineralization), a process that may take several weeks or months. This results in greater variability in mineral density between mature and more recent bone tissues in older individuals, especially in osteonal or Haversian bone (Ortner and Turner-Walker, 2003). There is an intimate association between the collagen molecules and HAP, and this chemical affinity is strengthened by the non-collagenous protein osteocalcin, which makes up 2 %

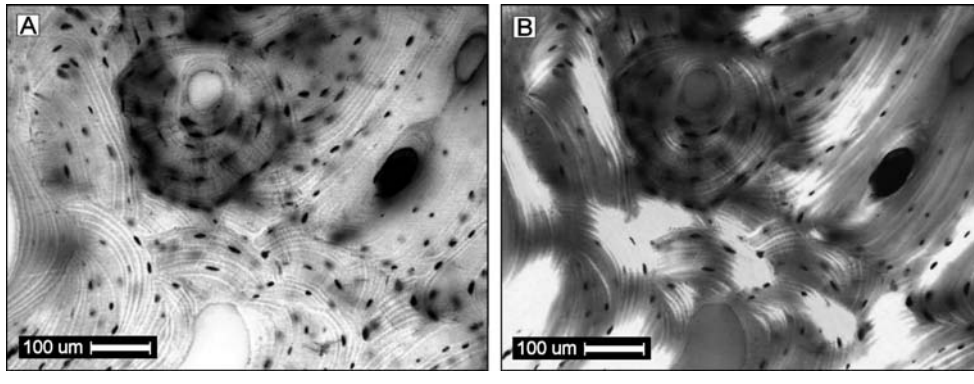

Figure 1.2 (a) Transmitted light image of medieval human bone from Trondheim, Norway. Histological preservation is excellent, but staining around the central osteon illustrates the fine canalicular network that connects the tissues with the soil environment. (b) The section viewed in polarized light with a quarter-lambda plate. The spectacular birefringence arises from the alignment of collagen fibrils and HAP in the bone lamellae

by weight of dry bone (Smith *et al.*, 2005). Osteocalcin is known to bind both to HAP and to collagen, and this relatively small protein plays an important role in the primary mineralization of skeletal tissues.

Dry, fresh bone contains about 8 % water that is loosely bound and can be driven off by heating in air at 105°C (Eastoe and Eastoe, 1954). However, for materials like bone with a high microporosity, the total amount of bound water held by a sample depends strongly on both the temperature and local relative humidity. For very small pores, quite high temperatures are required to drive off all the liquid water held in small capillaries, and even higher temperatures are necessary for chemically bound water. Determination of total bound water in fresh bone is further complicated because, in thermogravimetric measurements, weight losses at elevated temperatures are compounded by thermal decomposition of organic matter and loss of bound carbonates from the bone mineral.

Measurements undertaken by Nielsen-Marsh and Hedges (2000a) of pore volumes for fresh bone using calibrated relative humidities indicated that the macroporosity (those pores with radii between 4 and 20 nm) and microporosity (pores less than 4 nm in radius) were 0.075 $cm^3\ g^{-1}$ and 0.059 $cm^3\ g^{-1}$ respectively, giving a total pore volume below 20 nm of 0.134 $cm^3\ g^{-1}$. This figure compares well with measurements of total pore volume for fresh, compact bovine bone, which lie in the range 21–26 % by volume or 0.110–0.158 $cm^3\ g^{-1}$ (data from Turner-Walker and Parry (1995)). These latter measurements (made from liquid water absorption) included larger pores attributable to vascular channels and voids left by degraded bone cells (osteocyte lacunae). More recently, mercury intrusion porosimetry has refined the interpretation of bone porosity in the range 2 nm to 100 μm, and this technique has had a significant bearing on current understanding of bone diagenesis (Nielsen-Marsh and Hedges, 1999; Turner-Walker *et al.*, 2002; Jans *et al.*, 2004).

Bone is a physiologically active tissue, repairing itself when damaged – either at a macroscopic scale, as during the healing of a fracture, or microscopically, as in the constant remodelling and replacement of bone to remove the microfractures that accumulate through normal activity. Bone is also involved in calcium homeostasis, releasing or absorbing Ca^{2+} ions to maintain serum calcium levels within physiological limits. This requirement for skeletal bone mineral to be immediately accessible hinges on both the large available surface area of bone HAP and the considerable vascularity of bones. Living bone is penetrated by numerous channels (Haversian canals and canals of Volkmann) averaging about 50 μm in diameter, through which pass blood vessels and nerves (Figure 1.3). The branching architecture of these vessels provides a pathway between the countless bone cells or osteocytes within the bone tissues and the circulating blood. A large number of cytoplasmic processes extend from each osteocyte, connecting to neighbouring cells via canaliculi with a diameter of approximately 200 nm. This extended network of fine channels penetrating bone allows chemical messages to be transmitted throughout the tissue, as well as permitting nutrients and mineral ions to be supplied to the bone matrix and metabolic waste products to be removed (Figure 1.2a).

The microarchitecture of bone tissue varies, depending upon where it forms and the speed at which it develops. Bone tissue associated with very rapid growth is called woven or fibre bone. Fibre bone is not as dense or as well organized as other types of bone associated with slower growth rates. The collagen microfibrils are irregular in thickness and lack the linear orientation typical of later stages of bone development. Fibre bone forms early in the growing skeleton but may be found in later life in abnormal bone tissue, such as fracture callus and neoplasms (cancers) or beneath the periosteum as a response to infection. Mature

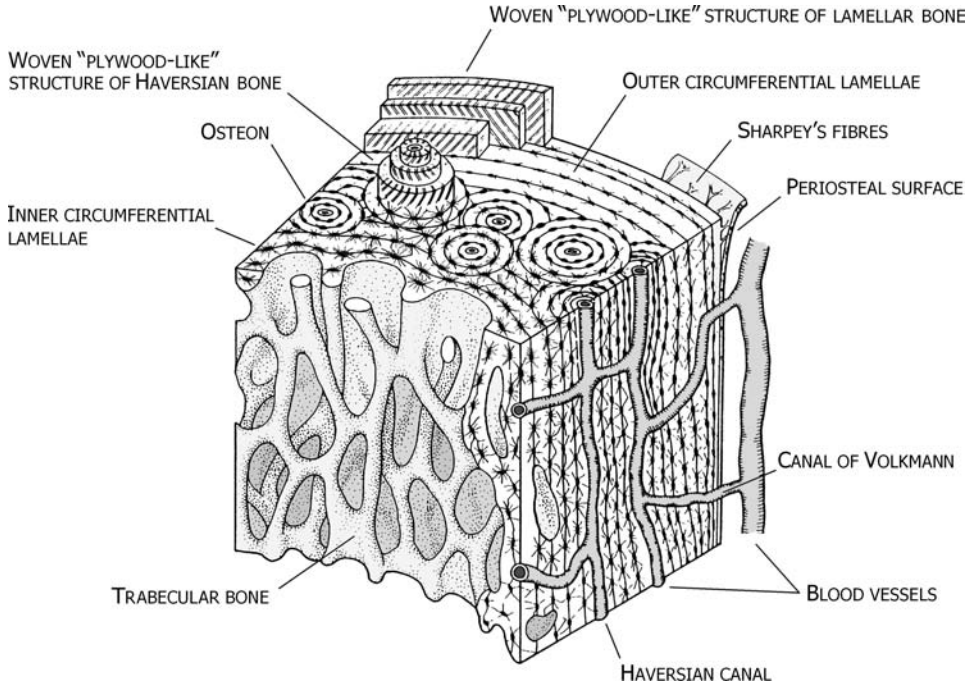

Figure 1.3 Three-dimensional representation of the micro-architecture of compact bone

bone has a more lamellar structure, forming either by apposition on the periosteal surface (circumferential lamellar bone) or by remodelling of the interiors (Haversian or osteonal bone). The microarchitecture of bone tissues clearly influences its mechanical properties, porosity and, ultimately, its resistance to post-mortem degradation. However, a detailed description of bone development and physiology lies outside the purposes of this chapter. For a fuller account of the biology of skeletal tissues the reader is referred to Ortner and Turner-Walker (2003) and Tuross (2003).

Tooth Dentine and Enamel

Teeth are complex structures that have properties that represent a trade-off between the need for a hard, resistant material that can efficiently withstand many years of biting or grinding tough foods and one that has good resistance to fracture. Good teeth are fundamental to the survival of any animal, and nature has perfected many different designs to suit different diets and feeding strategies. Unlike bones, which grow *in situ* and remain surrounded by soft tissues, teeth form within the jaw and are later erupted through the gum into the mouth, where they are in frequent and intimate contact with the outside world. Once in place, any remodelling or repair of damage is strictly limited because the tooth is effectively removed from the cellular apparatus that formed it. By way of compensation, humans develop two sets of teeth, the milk or deciduous teeth of infancy and the permanent teeth which gradually replace the deciduous teeth. The permanent dentition is complete by about 18 years of age.

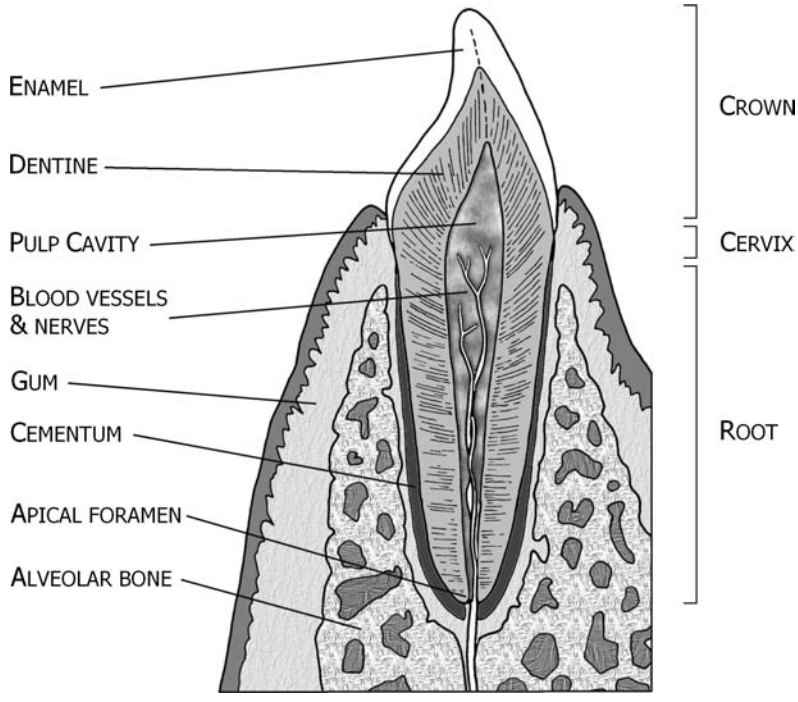

Figure 1.4 Simplified cross-section of a tooth (incisor) and jaw

The mature human tooth can be divided into three parts: the crown, which is the part visible above the gum; one or more roots, which anchor the tooth into the jaw; and the neck or cervix, where the crown meets the root and which lies between the gum-line and the socket (Figure 1.4). The bulk of the tooth is composed of dentine, which forms the underlying load-bearing structure. Unlike bone, dentine is an avascular tissue with no blood supply. It is also largely acellular and the living part of the tooth is restricted to the pulp cavity, which extends from a small hole or foramen in the base of the root into the body of the tooth. The pulp cavity contains blood vessels and nerves and is lined with cells called odontoblasts. Numerous, tightly packed dental tubules extend radially out from the pulp cavity towards the outer surfaces of the tooth. These tubules reflect the developmental growth of the tooth (in the growing tooth, dentine is laid down on the interior surface of the enamel and proceeds inwards) and provide a sensory mechanism for detecting loads on the teeth. The crown of the tooth is encased in hard enamel, which is made up of parallel prisms composed of almost pure HAP. Enamel has negligible organic content and is more crystalline than bone HAP as a result of a larger crystallite size and their parallel alignment within prisms. Once enamel is damaged by tooth wear or dental disease (caries) there is no natural mechanism for effective repair. The outer surface of the tooth root is covered in a type of woven bone called cementum which, together with the periodontal ligament, anchors the tooth in the socket (Mays, 1998; Ortner and Turner-Walker, 2003). Healthy enamel has zero porosity, apart from occasional growth defects. Although there has been little or no investigation of the porosity of tooth dentine, it is clear that its porosity is low compared with that of bone.