

Editorial 'The Human Biology of the Past'

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Introduction

Human biology and palaeoanthropology share common theoretical perspectives drawing on biological and evolutionary principles. As a result, studies in each field may incorporate many of the same research objectives, techniques, and questions about their populations, species, and specimens of study – some living, some long dead. The classic text *Human Biology: An Introduction to Human Evolution, Variation, Growth and Adaptability* (Harrison et al. 1988) embedded palaeoanthropology firmly within human biology, noting that palaeoanthropology and human biology share the same research aims in documenting the biological, adaptive, behavioural, and genetic characteristics of the species studied. In his contribution to *Human Biology*, Pilbeam (1988) identified different variables defining the scope of research questions about human and primate evolution, listing essentially the same biological, ecological, behavioural and reproductive traits that are of interest in research of the living; the aims in reconstructing the palaeobiology of extinct species are largely the same as those in studying living populations. The existence of these common research approaches is also evident in the membership and objectives of the Society for the Study of Human Biology (SSHB). Its 2013 symposium, 'The Human Biology of the Past', held in Durham, UK, aimed to explore the common ground between researchers working on 'past' and 'present', and formed the basis for the articles that feature in this special issue.

The trend towards academic specialism has resulted in a vast number of 'interdisciplinary' initiatives in universities around the globe (Chettiparamb 2007). Human biology has always been interdisciplinary, encompassing topics as seemingly diverse as genetics, growth and ecology. What unites these topics within human biology, and why human biology has always been and necessarily will remain a broadly-based discipline, is an emphasis on variation and adaptation. This emphasis allows research into the origins and evolution of our own species to fit very comfortably within human biology. The speakers and participants in the symposium - and contributors to this volume - were drawn from an array of academic homes, including university and museum schools or departments of sport, exercise and health science, anatomy, archaeology, earth sciences and anthropology. Following Harrison et al. (1988), their topics can be divided into the synergising key areas of human genetics and variation, human and primate evolution, and human growth, composition and life history. Reconstructing the biology of past populations and species is far from trivial, however, when considering the fragmentary nature of the archaeological and fossil records. The contributors to this volume utilise data and approaches drawn from studying living populations of humans and primates to illuminate the past through analyses of the archaeological and osteological records, and research into extinct hominin species. The articles in this volume approach

human biology, in its broadest sense, in several different ways to provide windows onto the past: study of fossils (Dean and colleagues, Stringer and Buck), examination of genetic and morphological diversity in modern populations (Mastana, von Cramon-Taubadel), theoretical insights from studies among living populations to address questions about human evolution and life history (Winder and Winder, Bogin and colleagues), and research on how the microstructure of hard tissues such as bones and teeth may document pivotal life history events such as pregnancy and weaning (Dean and Elamin, Humphrey). This special issue aims to show how ideas, data, and research techniques can move from one sphere to another, addressing how studies of living and past species inform and enhance each other, and the ways in which work on living populations provides a foundation from which to extend research into past populations and extinct species.

Human Genetics and Variation

Studies of the population genetics of living humans contribute to our understanding of the past by revealing the movements and population structure of ancient groups. These in turn help to reveal more about the human biology of the present and future, particularly disease prevalence and experience. In this volume, Mastana reviews research into the population genetics of India – which he describes as a “treasure for evolutionary biologists and geneticists” (Mastana 2014 p:x) – to illustrate how genetic insights into the past reinforce knowledge of the present. The high levels of genetic diversity in modern India are a product of multiple interacting factors. Waves of historic immigration into the sub-continent added to the diversity present in the early indigenous populations. Social structures – particularly the caste system – created distinct endogamous population groupings, creating genetic heterogeneity in the total population. Reproductive isolation among castes, however, may have promoted some of the population-specific diseases found in India today. Mastana’s article shows very clearly the links between present and past human biology and in turn how appreciating those links may help to shape future research to aid the health and well-being of those living in one of the world’s most heavily-populated countries.

Asia is becoming increasingly prominent in palaeoanthropological as well as genetic study. With a history dominated by excavation and fossil collection in Africa and Europe, palaeoanthropologists have woken up to the fact that evidence from Asia has the potential to transform how we view human evolution. The very recent, diminutive *Homo floresiensis* showed that adaptive radiation in the hominin lineage extended well into the Pleistocene (Brown et al. 2004). It also emphasised that our own species, *Homo sapiens*, probably lived alongside multiple congeners. The discovery in central Asia of a new *Homo* lineage, the Denisovans, with a fossil record that could fit inside a

matchbox but a mitochondrial genome that appears distinct from modern humans (Krause et al. 2010), also revitalised interest in possible interbreeding between hominins assigned to different species (Reich et al. 2010). Such reticulation, argued by Winder and Winder in this volume, is likely to have been much more common in the evolutionary history of our species than is normally acknowledged. Using examples of reticulate evolution from plant and other animal species, including non-human primates, they highlight the potential importance of non-hierarchic processes in human evolution. Models and interpretations about human and primate evolution, species recognition, and population dynamics among extinct organisms may well undergo a profound shift as more is discovered about genetic diversity and hybridisation within our own lineage in the past.

Human and Primate Evolution

It could be said that this special issue itself is reticulated, such are the multiple links between topics and also between lines of evidence from present and past populations. Synergies between topics in this volume are no more evident than when considering reticulate evolution. Taking a different perspective on the species boundaries of *Homo sapiens*, based on the fossil record but integrating archaeological and genetic evidence, Stringer and Buck provide considerable insight into diagnosing our own species. They conclude that although genetic diversity is a “patchwork” (Stringer and Buck 2014 p. x) and morphological boundaries may be fuzzy, vital distinguishing traits for the *Homo sapiens* lineage can nonetheless be identified in fossils. This is highly relevant in examining the human biology of the past. By separating early and more recent *Homo sapiens* within the evolving lineage, differences in enamel thickness and microstructure, pelvic morphology and inner ear form become evident (reviewed in Stringer and Buck 2014), which indicate adaptive shifts in biology and behaviour through time. Assessing a mainstay of human biology, biological variation (although a highly challenging task when working with the fossil record), should also be more straightforward when organisms can be grouped. However, taking the most straightforward course is not necessarily desirable, as suggested by Winder and Winder (2014) in their critique of the dominant palaeoanthropological (and, indeed evolutionary biological) paradigm that requires hierarchical grouping. The philosophical differences evident in their contribution and that of Stringer and Buck provide stimulating reading and show how disciplinary perspective influences our reading of past human biology, including the ways in which ‘human’ might be defined in these investigations.

Further ‘reticulation’ and synergies between genetics and morphology are evident in von Cramon-Taubadel’s contribution to this special issue, in which she critically reviews the growing literature on how cranial variation may reflect past population history. Understanding the processes that shape

morphological diversity is vital in the efforts to reconstruct the evolutionary relationships between organisms accurately using evidence from body form. This endeavour, as pointed out by von Cramon-Taubadel, has been fraught with difficulty, not least because we still have insufficient knowledge about how both micro- and macroevolutionary processes give rise to the morphological patterns seen in extant primates. “Understanding the (evolutionary) human biology of the past..” she states “...requires a comprehensive understanding of evolutionary biology in the present” (von Cramon-Taubadel 2014, p. x). Von Cramon-Taubadel presents a compelling argument that trying to find morphological regions that consistently recover a phylogenetic signal across all primates may be fruitless, and instead researchers should pay more attention to congruence in signal from varied types of evidence (for example, different parts of the skeleton) as well as assessing the evolutionary forces that act to create morphological differentiation within groups. Her contribution stands as a reminder that when examining the human biology of the past, a ‘one size fits all’ model is far from appropriate.

The detailed study of pattern and process advocated by von Cramon Taubadel is evident in the contribution by Dean, Liversidge and Elamin. By combining radiographic and histological data on canine development from a comparative human sample, they estimate the age at death of one of the most iconic hominin fossils, the Nariokotome Boy (KNM-WT 15000). Through comparing stature and mass estimates of KNM-WT 15000 to those of modern Sudanese children at a similar age, it appears that the Nariokotome Boy was much bigger, which although would be more energetically costly, may have been a worthwhile trade-off in the face of, for example, predation risk. Dean et al.’s meticulous study shows how modern human biology can be used to reveal aspects of past human biology. It is also an example of how such data can provide a framework not only for reconstructing the ‘basic’ biology of extinct hominins – such as maturation and relative body size – but also provides a window onto their ecology, behaviour and life history.

Human growth and life history

Research on human growth and life history in living populations can incorporate the study of large numbers of individuals throughout their lives, and can evaluate aspects of growth, maturation and body composition in the context of differences in environment, fecundity, fitness and other life history parameters. The availability of large samples and varied population groups helps to deepen our understanding of the many factors affecting life history and fitness. In contrast, research on the evolution of life history in extinct species relies largely on estimation based on a few hard tissue variables from definitively cross-sectional samples – dental development, body size and brain

volume – that are known to generally reflect life history schedules, but do not provide direct insights into other important aspects of life history (Robson and Wood, 2008). How, then, can human biologists, evolutionary primatologists, and palaeoanthropologists develop research strategies for reconstructing life history in extinct species that go beyond the few hard tissue variables available from the fossil record and shed light on social and reproductive aspects of early hominin life history? One aspect of most research about the evolution of human growth and life history is the reliance on new technologies to extract remarkable details from preserved hard tissues such as bones and teeth (Smith and Tafforeau, 2008). To a large degree, such research incorporates studies and samples from (recently) living populations of humans or primates in order to produce comparative standards for a variety of growth processes that can be also be identified in the fossilized hard tissues of extinct species. The papers in this special issue demonstrate that research continues to push the boundaries that allow access to intimate details about the lives of long-dead individuals.

Humphrey's contribution to this special issue is an excellent example of the use of data and techniques in the living to illuminate our understanding of past populations and species, and to unlock information that has previously been unavailable to bioarchaeologists and palaeoanthropologists. It is relatively straightforward to document the age of weaning in living populations, and to record the dietary changes that occur before and after the weaning period. These data are critical to understanding differences in reproductive strategy, fitness, and life history in different species, but are essentially impossible to estimate reliably in extinct species without a hard tissue `surrogate` for direct behavioural observation. Humphrey's article shows the complexities surrounding how dietary changes before and after the weaning can be reconstructed using microsampling techniques for stable isotopes and mineral trace elements preserved in skeletal and dental hard tissues. Clearly, it is necessary to study these processes in living species and populations in order to develop methods for application to extinct human samples or species. This area of research has the added potential to document human biological change through time, or among populations, to understand the differences and impact of past and contemporary practice in weaning behaviour. Dean and Elamin, in this volume, also focus on the use of dental structures in palaeobiology to predict events that cannot be directly observed in skeletal or fossil material – this time to provide further insights into the individual life histories of extinct hominins. As shown in Humphrey's contribution, one big challenge when reconstructing past human biology is to tease out the reliability of the relationship between life history variables and those variables that are less directly life history-related, but which can be identified in skeletal and fossil remains (Robson and Wood, 2008). Dean and Elamin focus on identifying whether parturition lines in M3 root dentin (a

'related' variable) are present in living women with known reproductive histories, to ascertain whether teeth give an accurate picture of birth events (a life history variable). While the results are not conclusive, they indicate that parturition lines corresponding to childbirth during the teenage years can exist in human M3 roots but may not always be present. This work provides stimulating prospects for further development of a technique to determine age of first reproduction in extinct populations or species – again, using a living model to improve and broaden the scope of palaeobiological reconstructions.

There are many routes to reconstructing past human biology. Humphrey and Dean and Elamin focus on evidence from hard tissue. In contrast, Bogin and colleagues present a thought-provoking theoretical discussion of the unique human reproductive system, introducing a biocultural approach to explain its adaptive basis and success. There is much potential such rich theoretical models about the evolution of human life history to be used in combination with practical research to shed light on the past. The fundamental basis for Bogin et al.'s model is that "human care and provisioning for the offspring of others is not governed by the close genetic relatedness found in all cooperative breeders, but is structured by sets of local, culturally-defined rules" (Bogin et al. 2014, p. xx). Factors such as alloparenting and paternal support (sometimes, but not always involving monogamous marriage practices) serve to reduce mothers' lifetime reproductive effort, and allow for the observed increase in offspring produced, and perhaps contribute to lifespan extension. Their article provides a feasible explanation for the unique features of modern human reproduction and childcare behavior, as well as the adaptive and evolutionary context for its origin.

Conclusion

The articles in this special issue are wide ranging and varied, demonstrating the breadth of approaches that can be used to reconstruct the human biology of the past. The symposium itself was filled with fruitful discussion and conversation between researchers working in different topical and methodological areas. One of the primary features of this collection of papers is the valuable interplay between theoretical or comparative frameworks from human biology on the one hand, and the technological challenges of producing the evidence needed to test and refine existing palaeobiological models on the other. We hope that the articles in this volume this will help to promote a greater degree of dynamic interaction, and stimulate further discussion of the various forms of engagement and interaction that are possible between human biologists, palaeoanthropologists, and other researchers.

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