



Human Palaeontology and Prehistory (Palaeoanthropology)

## The principles and practice of human evolution research: Are we asking questions that can be answered?



*Principes et pratiques de la recherche sur l'évolution humaine : nous posons-nous des questions auxquelles nous pouvons répondre ?*

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## ABSTRACT

The research agenda of paleoanthropology involves many topics and methodologies. Fossil specimens are allocated to species, and those species are assigned to the hominin clade. After that we want to know how they are related to each other, what they ate, how much they weighed, how smart they were, etc. We also want to know about the origin of particular attributes of hominins, such as our delayed growth and development, bipedalism, and language. The data available to answer these complex questions are confounded by fragmentary fossil specimens, small sample sizes, limited opportunities for controlled experimentation, and the inherent limitations of historical data. Also, because many traits are effectively unique to hominins, even observational comparative studies are inevitably limited in what they can tell us, if not impossible to conduct. We explore how these limitations should, but often do not, constrain the questions that paleoanthropologists should attempt to answer.

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## R É S U M É

Le programme de recherche en paléanthropologie comporte de nombreux sujets et méthodologies. Les spécimens fossiles sont rapportés à des espèces, et ces espèces sont assignées au clade des hominins. À présent, nous cherchons à connaître comment celles-ci sont reliées entre elles, quelles elles sont, quels étaient leur poids, leur élégance, etc. Nous souhaitons aussi connaître l'origine d'attributs particuliers des hominins, tels le retard de croissance et de développement, la bipédie et le langage. Les données disponibles pour répondre à ces questions complexes sont fournies à la fois par des spécimens fossiles fragmentaires, des échantillonnages de taille réduite, des opportunités limitées pour le contrôle des expérimentations, des limitations inhérentes aux données historiques. Ainsi, bien que nombre de traits soient effectivement propres aux hominins, même des études descriptives comparatives sont inévitablement limitées en ce qu'elles peuvent nous apprendre,

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voire impossibles. Nous explorons ici combien ces limitations risquent ou non de contraindre les questions auxquelles les paléoanthropologues tenteraient de répondre.

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## 1. Introduction

The authors of this review have, between them, more than 80 years of experience in human evolution research. Both were trained in clinical disciplines before their Ph.D. (RJS as an orthodontist and BW as a surgeon), and both were deeply involved in teaching dental and medical students, and in administration within dental and medical schools. Perhaps the contrast between the nature of scientific evidence necessary in preclinical and clinical practice and research with our experiences in paleoanthropology, led both of us to work primarily on developing a more realistic understanding of what can and cannot be gleaned from the existing fossil record. In this report, after briefly summarizing the scope and objectives of human evolution research, we consider whether the categories of questions commonly addressed using fossil data are realistic given the limitations of the data available to human evolution researchers. Paleoanthropologists are not alone in dealing with contingent, complex, and unique historical events. Among others, cosmologists, astrophysicists, geologists, archaeologists, epidemiologists, and historians share some of our methodological complexities and limitations, and there is much to learn from their insights.

## 2. The scope of human evolution research

By the early 1960s, a new generation of analytical methods became available to investigate the relationships among modern humans and the apes. Zuckerkandl (1963) and Zuckerkandl et al. (1960) broke up the globin component of the hemoglobin molecule into its components, and showed that the patterns made in starch gels by the peptides from modern humans, gorilla and chimpanzee were indistinguishable. Goodman (1962, 1963) used immunodiffusion to show that the patterns produced by the albumins of modern humans and the common chimpanzee were also indistinguishable, leading him to conclude that their albumin molecules were for all intents and purposes identical. Sarich and Wilson (1967) used molecular differences to suggest it was only c.5 Ma since the split between modern humans and the apes, and King and Wilson (1975) found that 99% of the amino-acid sequences of the chimpanzee and modern human blood proteins they examined were identical.

Nowadays, relationships among organisms can be pursued at the level of the genome, thus eliminating the need to rely on proxies be they traditional phenotypic morphology, or the morphology of proteins, for information about relatedness. Technological advances mean that whole genomes can be sequenced, and over the last decade, or so, researchers have published good draft sequences of the nuclear genomes of the chimpanzee (Chimpanzee Sequencing and Analysis Consortium, 2005), the orangutan

(Lock et al., 2011), the gorilla (Scally et al., 2012) and the bonobo (Prüfer et al., 2012). Meanwhile, better quality data and larger data sets (e.g., de Manuel et al., 2016; Gordon et al., 2016; Prado-Martinez et al., 2013; Xue et al., 2015) are being accumulated. Scally et al. (2012) showed that, across the genome, the greatest number of similarities between modern humans and the African apes are those between modern humans and chimpanzees/bonobos. This is consistent with the results of the earlier analyses reviewed above, which suggested that modern humans and chimpanzees are more closely related to each other than either is to the gorilla.

If these differences in DNA are calibrated using paleontological evidence for the split between the apes and the Old World monkeys, and depending on the assumptions one makes about the extent of neutrality, generation times (e.g., Langergraber et al., 2012), mutation rates (e.g., Venn et al., 2014), life history (Amster and Sella, 2016), and other potential confounding factors, researchers presently suggest the hypothetical ancestor of modern humans and chimpanzees/bonobos lived between about 9 Ma and 6 Ma (Amster and Sella, 2016; Moorjani et al., 2016), with some favoring the recent end of this range (Prado-Martinez et al., 2013), and others the older end (Moorjani et al., 2016).

So, the remit of human evolution research is to improve our understanding of the twig (aka clade) of the Tree of Life (ToL) that links the most recent common ancestor of modern humans and chimpanzees/bonobos to modern humans. In addition to the direct ancestors of modern humans, there is compelling evidence that the twig also includes non-ancestral species that are judged to be more closely related to modern humans than to chimpanzees/bonobos. Human evolution research involves recovering, sorting and analyzing the relevant paleontological evidence to try to identify, distinguish, and characterize species (Wood and Boyle, 2016), and then decide whether any of those extinct species are actual ancestors, or just close relatives. After that, researchers use the phenotype to learn as much as they can about the growth and development and functional biology of each species (see below). It is becoming conventional to include the extinct species within the hominin clade, along with modern humans, within the tribe Hominini, so in this contribution we refer to the individual taxa, and the individuals in those taxa, as hominins. Similarly, chimpanzees/bonobos, and their direct ancestors and close relatives, are panins.

But how do you decide whether an extinct species belongs within, or is just close to, the hominin clade? There are an impressive number of differences between crown hominins (modern humans) and crown panins (chimpanzees/bonobos), so it is not difficult to identify potential ancestors and close relatives within the later hominin fossil record. But the differences between the earliest hominins and the late Miocene ancestors of chimpanzees/bonobos

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