



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 ?

Richard J. Smith^a, Bernard Wood^{b,*}^a Department of Anthropology, Washington University in St. Louis, St. Louis, MO, USA^b Center for the Advanced Study of Human Paleobiology, George Washington University, Washington DC, USA

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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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* Corresponding author.

E-mail address: bwood@gwu.edu (B. Wood).

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 (Sally 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. Sally 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

are likely to have been much more subtle. Some of the features that distinguish modern humans and chimpanzees/bonobos, such as those linked with bipedalism, can be traced back a long way. Others, such as the relatively diminutive jaws and chewing teeth, and the larger brains, of modern humans were acquired more recently and thus cannot be used to tell the difference between early hominins and the ancestors of chimpanzees/bonobos. The presumption about the early members of the hominin clade is that they would have cranial and other skeletal adaptations for a predominantly upright posture, and a locomotor strategy that includes substantial bouts of bipedalism. These features would be combined with a masticatory apparatus that combines relatively large chewing teeth and more modest-sized canines. These inferences, which are working hypotheses that depend on a number of assumptions, will need to be reviewed, tested, and revised, as relevant fossil evidence is uncovered.

But the presence of only one, or even a few, of the features that possibly distinguish early hominins from early panins, may not be sufficient to identify a fossil, or a species, as hominin or panin. This is because there is evidence that primates, like many other groups of mammals, are prone to homoplasy, which is morphology shared by two, or more, taxa that is *not* seen in their most recent common ancestor (Jolly, 2001; Lockwood and Fleagle, 1999). Homoplasy means that it is not impossible, indeed it may even be probable, that some of what many have come to regard as key morphological adaptations at the base of the hominin clade may have arisen more than once. If that is the case, then what characterizes hominins and panins may not be particular items of morphology (i.e., single characters) but combinations of characters. Homoplasy also has the potential to confound attempts to reconstruct the relationships among hominin taxa (see below).

There is also the additional potential complication that being an ancestor of modern humans or chimpanzees/bonobos is not the only option for hominin and panin-like taxa. They could belong to closely related clades that have no living representative. So labeling *any* taxon, especially one that has a poor fossil record and that only samples a few individuals, as one of the earliest members of the hominin clade is always going to be a risky enterprise. For a taxon to be a viable candidate as an early hominin, several aspects of its morphology need to be features that we can be certain are only seen in true hominins.

3. The objectives of human evolution research

Once researchers have decided what fossil evidence to include within the hominin clade, the next task is to generate reliable alpha taxonomic hypotheses about how many species are sampled by the hominin fossil record. Then, if multiple species are recognized in the same time period, we also need to work out how they are related, and determine which, if any, are our ancestors, and which are non-ancestral close relatives. We also want to use our knowledge of the phenotype of each of the species we choose to recognize to find out as much as we can about other aspects of its biology. How tall were members of the species? How much did they weigh? What size brains

did they have? How much sexual dimorphism was there? How quickly did they develop? What was the predominant resting posture? How did they move around? How dexterous were they? To what extent, and how, did they communicate? What was their level of cognitive development? Were they social, and if so, how did their societies function?

It is also tempting to try to answer “origins” questions. For example, when, where, how and why did hominins acquire the distinctive morphological features of modern humans, such as our large brains, the distinctive morphology and proportions of our limbs, and our delayed growth and development? When, where, how and why did we acquire the morphology that enables the distinctive behaviors of modern humans, such as our upright posture, bipedal locomotion, manual dexterity, theory of mind and the ability to communicate and plan using complex spoken language? In terms of “why” questions, it has been traditional to interpret events in human evolutionary history in an environmental context. If tooth size and morphology were changing, “why” did they change? What types of habitat were our ancestors spending their time in before and after any change? Did changes in habitat preference drive that change? Were such changes driven by changes in climate (e.g., deMenocal, 2011)? Various lines of evidence – genetic, archeological and ecological – can be brought to bear to help answer questions such as the ones posed above, but in this review, we are going to focus on the fossil evidence, and what can be reasonably inferred from it.

4. The nature of the data

Before we explore the nature of the questions addressed by those seeking to interpret the hominin fossil record, it is worthwhile reminding ourselves of the many factors that determine what that fossil record consists of. Taphonomy is the study of the factors that intervene between a once living population and its fossil evidence (Behrensmeyer and Kidwell, 1985). For example, some parts of the hard-tissue skeleton are denser and more durable than others, and in general the more durable a structure is the more likely it is to be represented in a sample of hominin fossils. Factors like differential preservation of remains, time averaging and collection biases combine to obscure the fidelity with which fossil collections reflect the original animal community they sample (Behrensmeyer et al., 2000). Depositional environments, for example cave sites versus open-air sites formed in the vicinity of rivers and lakes, as well as the skeletal preferences of predators, also influence the sorts of individuals, and the parts of the body, that are likely to find their way into the hominin fossil record. When researchers compare variables (e.g., body size, body mass, brain size, tooth size) among hominin fossil taxa, they either implicitly assume the fossil samples are an unbiased sample of each taxon, or they acknowledge that the samples are biased, but assume that the biases are the same across taxa. But, to what extent are such assumptions justified, especially if one taxon comes from a cave site, and one from an open-air site. For example, if the individuals at one site are dominated by the prey of smaller predators then that site may

be biased in favor of smaller-bodied females, whereas the individuals that make up a collection of another taxon at a different site may be dominated by larger-bodied males. If this were the case, inter-taxonomic comparisons of the mean values of variables used to estimate body mass would be of questionable value.

5. Asking answerable questions

We have reviewed the diversity of questions paleoanthropologists ask about the past. Our concern is that there are systematic constraints on the types of questions we can answer about the past, yet these constraints have not prevented human evolution researchers from generating answers to questions that cannot be answered [e.g., implying or inferring “cause and effect” links between fluctuations in regional and global climates and events in human evolution (e.g., Anton et al., 2014; Potts, 2012), with no way of empirically evaluating such links]. This is a significant problem because one of the key ways in which science differs from other forms of knowledge generation is that its theories are based on hypotheses that can be falsified with empirical, reproducible evidence. Others have recognized this problem, and it has led to some soul-searching concerning the scientific credibility of paleoanthropology. For example, Washburn (1973) asked whether the study of human evolution is a “science or game”, and Cartmill (2002) pondered whether it is “science or mythological charter”.

It is our view that science is a “big-tent”. Progress is made through unexpected means, through originality, and individual research projects need not conform to narrow criteria of what differentiates science from other forms of knowledge, or perhaps even from pseudoscience. Individual studies need not be falsifiable or confirmable. They may be descriptive, and they may have utility even though they pose questions that may not be answerable. Nonetheless, the overall research agenda of a discipline such as palaeoanthropology must conform to science norms. This means, among other things, that it provides answers to testable questions (by confirmation, falsification, and/or prediction), that it seeks generalizations (i.e., laws), and that its knowledge is cumulative and progressive. Lest we wish to be categorized with astrology, phrenology, and tarot reading, paleoanthropologists cannot embrace a core research agenda that regularly concerns itself with untestable theory-driven questions for which alternative answers cannot be differentiated on the basis of the available, or potentially available, evidence.

We argue here that too many of the questions that are an accepted part of the research agenda in paleoanthropology should not be asked – because it is clear that they cannot be answered in a way that conforms to accepted scientific standards. We discuss below a group of interrelated issues that contribute to the limitations of scientific explanation in paleoanthropology. These issues help to identify questions that paleoanthropologists should avoid, but sometimes the temptation to address unanswerable questions has proved to be irresistible.

6. Explaining unique traits

We define a feature or a trait to be “unique” when an investigator concludes that there are *no* comparative data against which the feature can be evaluated, interpreted, or contrasted. Uniqueness is an all-or-none phenomenon; there are no degrees of uniqueness. By definition, just as a historical event is blocked from experimental evaluation, a unique feature, trait or event is blocked from direct comparative evaluation.

The idea of modern human uniqueness is both philosophical and empirical. “Human uniqueness” means different things to different scholars, yet it has a long history of being embedded, either explicitly or implicitly, into our understanding of human evolution (e.g., Bingham, 1999; Cartmill, 1990, 1993; Hill et al., 2009; Huxley, 1941; Lang et al., 2002; Tattersall, 1998; van Huyssteen, 2006; Varki et al., 2008). The assumption that modern humans are different has much basis in fact. However, the uniqueness attributed with some justification to modern humans becomes less and less appropriate as we move back in time to a last common ancestor shared with chimpanzees and bonobos. We think most investigators would agree with this distinction. However, it appears that the assumption of uniqueness creeps into thinking about early human ancestors as an unjustified generalization about the characteristics of the “human lineage”, whether that term is interpreted to mean the whole of the hominin clade, or just the presumed ancestors of modern humans.

It is commonly understood that at some level every item and every event that has ever occurred is “unique” (Fetzer, 1975). Every snowflake that has ever fallen is different from every other one. Every modern human is different from every other modern human. But this does not stop us from studying snowflakes or modern humans as groups. Things and events that are unique in some respects can be studied in groups when in other respects the features of interest are examples of a type or class (Joynt and Rescher, 1961). Uniqueness is not an inherent property of an item. It is a decision about how to categorize its properties of interest, and it is sensitive to scale. The consequences of considering an object of study to be unique rather than a member of a group has major practical and philosophical implications that are often unappreciated (Smith, 2016).

The most problematic issues with the scientific understanding of a unique historical event arise with “why” questions. To question “why” a species appeared, or a trait evolved, is to seek a causal explanation for its presence, either with or without assumptions or, in the case of a trait, evidence of adaptation. Causation is certainly one of the most complex topics in epistemology and philosophy of science, but a general conclusion from this literature is that unlike questions of “who”, “what”, “when”, “where”, or “how”, a “why” question about a unique historical event cannot be resolved within the widely recognized and accepted requirements of evidence and falsification that demarcate science.

The argument is sometimes made that scientists often explain unique events, even historical ones, implying there is nothing special about them doing so (often accompanied

by the observation that “everything is unique”). We examine two examples – the K/T boundary and the big bang – commonly employed to counter the argument that there are fundamental limitations on the explanation of unique events. Indeed, the explanation for the K/T boundary is recognized as an exceptional scientific achievement (Alvarez et al., 1980). However, a scientific discussion of the K/T boundary does not include “why” the meteor impact occurred near what is now Yucatan, Mexico, rather than in Siberia or Australia. Nor “why” the impact occurred 66 millions of years rather than at some other time. It seems to be understood by scientists who study the K/T boundary event that these are not questions that can be addressed scientifically. Moreover, for the K/T boundary, we have physical and chemical laws that explain some of the many traces of the event that continue to exist in the present. These laws create testable predictions for aspects of the K/T boundary event that are *not* unique.

Explanations for events in human evolution present an entirely different kind of data set. Consider, for example, the origin of bipedalism. The law we can refer to is natural selection, which is contingent rather than determinate and does not allow for specific predictions. The event leaves no traces other than the event itself. There is much we can know, or eventually, explain about bipedalism – we can document that it evolved, interpret some of its biomechanical and physiological consequences, and with the right kind of additional evidence perhaps explain where, when, and in what sequence the anatomical changes occurred. But to explain *why* it evolved, which paleoanthropologists seem determined to do, is to ask an unknowable question of the sort that has been avoided with respect to the K/T boundary.

The big bang is an example of an explanation for a unique event that involves a different set of issues. The claim that we have “explained” the origin of the universe through the mechanism of the big bang is a confusion of description with explanation (Cartmill, 2013). Descriptions “give an account” of an event and in doing so they reveal both *that* it happened and *how* it happened. Explanations present the cause or reason for the event, thus they try to answer the *why*-question (Reese, 1999). Astrophysicists seem to have understood that asking why the big bang occurred would involve leaving the realm of science for something quite outside of it.

It appears to us that, unlike scientists examining the K/T boundary or the big bang, paleoanthropologists have not always demonstrated an appreciation for this distinction. Given limitations recognized at the outset of an investigation, it should be recognized that a “why” explanation of a unique historical event is the subject matter of history, not of science. Moreover, explanations for the unique historical events that are the landmarks of human evolution confront an extreme level of the “underdetermination problem” (see below). Simply put, there are multiple equally plausible answers to the “why” questions we try to answer. Alternative explanations cannot be differentiated because there is no evidence that effectively distinguishes them. Therefore, because they are unresolvable (i.e., unknowable) any attempt to answer them is not a scientific research agenda.

7. Science, or history?

The problem of defining “science” has occupied philosophers for generations. It is often identified as the “demarcation problem” – how to distinguish scientific research agendas from non-scientific ones (pseudoscience). For example, how does evolutionary biology differ from creation science? Some definitions of science focus on culture – such as describing science as requiring a community of interacting individuals submitting testable research to refereed journals. At the more relevant structural level, Lakatos (1977) suggested that “In scientific reasoning, theories are confronted with facts; and one of the central conditions of scientific reasoning is that theories must be supported by facts”. But the key question for our purposes is not the demarcation between science and pseudoscience. Instead, it is a question that has received much less attention, namely the demarcation between science and history.

As described by Gallie (1955, p. 160) “history is concerned with particular facts, with what actually happened on this or that particular occasion, whereas the natural sciences are concerned with specimen or sample facts and with what is sure or likely to happen on any occasion of given definite description”. Similarly, Joynt and Rescher (1961: 153–154) observe: “the object of the science is the study of a certain range of basic ‘fact’ with a view to the discovery of generalizations, ideally universal laws. . . particular facts have a strictly *instrumental* status for the sciences. . . In history, on the other hand, this means-end relationship is, in effect, reversed. . . History seeks to provide an *understanding of specific occurrences*. . . the role of generalizations is strictly instrumental; they provide aids towards understanding particular events. The scientist’s means-end relation of facts to laws is thus inverted by the historian”.

These distinctions between science and history are perhaps too stringent for questions of where, when, or how a historical event occurred. These, we believe, may be suitable subjects for scientific enquiry, but for “why” questions, the distinction holds. It is clear to us that the paleoanthropologist interested in “why” bipedalism, or large brain size, or hairlessness, or language, or secondary sex characteristics evolved should recognize that their question is analogous to problems of history, not of science. Paleoanthropologists certainly tend to identify themselves as scientists, but whether we are doing science is not determined by self-perception, but rather by the nature of the hypotheses, data, methods, evidence, and inferences we use. As discussed by Tucker (1998: 76), “The properties of events in conjunction. . . with the formation of the why-question decide the possibility of scientific explanation”. Thus, the question for paleoanthropology perhaps is not whether it is a science, game, or mythological charter (Cartmill, 2002; Washburn, 1973), but when is it science, and when is it more like history?

8. The underdetermination of unique events

A second fundamental issue with a research agenda involving the explanation of unique historical events is the fact that these explanations are characteristically

underdetermined. Underdetermination is a complicated issue in the philosophy of science, but straightforward in its implications for this discussion. Underdetermination occurs when two or more explanations for an event are equally compatible with all of the available evidence, even perhaps with all of the evidence that one could contemplate obtaining in the future. There is simply no objective way – based on the evidence – to choose between the alternative explanations.

There is a line of argument within the philosophy of science that all explanations are underdetermined, that there are always empirically equivalent alternative explanations for an event. This does not require the preposterous – such as that an alien spacecraft is responsible. Even so, this general argument is not relevant to the practice of science. We know empirically that science solves problems and exhibits cumulative knowledge, and that scientific explanations can lead to predictions that can be confirmed. Our concern with underdetermination is when a science (namely, paleoanthropology) pursues a research agenda that we should recognize will result in an untestable explanation that, for the foreseeable future, cannot be distinguished from other equally plausible explanations. As discussed by Bergström (1993: 338–339), “It would be very odd indeed if scientists should try to construct empirically equivalent and equally good alternatives to existing theories. . . Surely, the whole point of scientific activities is to find theories that are *better* than the theories that exist already. . . As soon as two theories appear to be empirically equivalent, equally good, and irreducible – and especially if they are also logically incompatible – we may expect scientists to make it their business to show that one of them is better after all”.

Our concern is that what Bergstrom suggests would be odd is routine within paleoanthropology. Underdetermination can be a problem in many circumstances. The issue for palaeoanthropology is that it is a *guaranteed* problem for causal explanations (answers to the question “why”) for a unique historical trait (Tucker, 1998). The idea that the question can be answered in any constructive way is predetermined to fail. As explained by Lang et al. (2002: 667–669) (italics added), “*testing* causal hypotheses requires a comparison of different types of cases – of situations in which dosages of the putative causal factor are different – helps explain [. . .] To test causal hypotheses about the place of human beings in nature, the human traits under study must be commensurable with the traits found in other species [. . .] suppose human beings are the *only* species that exhibits trait E. If so, there is an easy recipe for finding causal hypotheses that fit the data – merely find a trait C that also is unique to human beings. The result is that C and E will be perfectly associated [. . .] the hypothesis ‘C₁ causes E’ will fit the data, but so will ‘C₂ causes E’, ‘C₃ causes E’, and so on [. . .] the data sets used to test adaptive hypotheses *must* contain variation.”

This is also emphasized by Gerring (2004: 342), who noted (italics added): “*All* empirical evidence of causal relationships is covariational in nature. A purported cause and effect *must* be found to covary”, and by Tucker (1998: 65–66) who points out that “there are no acceptable scientific theories that can explain unique events. . . all possible theoretical backgrounds that are relevant for its

explanation. . . can have only a single positive confirming case, the event itself”.

The statistical interpretation of this problem is that with one observation ($N=1$) there are negative degrees of freedom for distinguishing between any two explanations (George and Bennett, 2005: 28). This is deeply at odds with the most fundamental historical understanding of science. McMullin (1995) refers to 17th-century arguments by Johannes Kepler that “saving the phenomena” with a hypothesis that simply predicts the data at hand is unacceptable; any *ad hoc* invention could do that.

9. Unconceived alternatives

Underdetermination has implications not only for competing hypotheses, but also for circumstances in which there appears to be consensus around a single hypothesis. As discussed by Stanford (2006), the history of science provides countless examples of apparently successful theories that turn out to be profoundly mistaken and replaced over time by alternatives. The history of science cautions us not to believe that even highly supported theories with strong predictive confirmation are “true”. Unless we wish to take the position – and it would be extraordinarily odd for an evolutionary biologist to do so – that our knowledge of the hominin fossil record has reached an “end of history” state, we need to accept the lesson that what the future will bring are new fossils that we cannot even imagine today, which will lead us to see new stories summarizing the path of the human lineage. The discoveries at Liang Bua (Brown et al., 2005) and at Rising Star (Berger et al., 2015) are two relatively recent examples, and the deeper history of hominin paleontology also indicates that palaeoanthropology is no exception to the rule that the future will produce what are now unconceived alternatives (Cartmill et al., 1986; Washburn, 1950). To illustrate this we include two versions of Fig. 1, one illustrating the hominin taxa that were widely recognized in 1950 (Fig. 2), and one illustrating the hominin taxa that were widely recognized in 1990 (Fig. 3). In 1950, the taxa recognized in 1990 were unconceived alternatives, and in 1990, the taxa recognized in 2016 were unconceived alternatives. We rest our case.

As a discipline, paleoanthropology is in a weaker position with respect to the importance of unconceived alternatives than most of science. The key concepts for most scientific research agendas involve theories that are supported because they have been confirmed through successful predictions. One of the organizing questions for paleoanthropology is to describe the topology of the human evolutionary tree. To do this, we do not generate testable theories. We generate *post hoc* sequences for the specimens at hand. First we find fossil specimens, we group them into species, and then we “connect the dots” to describe the shape of the human evolutionary tree. We connect the dots without knowing how many, or what kind, of dots are currently missing from the “true” tree, or what the implications of those missing data will be. We tell the story as we know it, knowing with certainty, if the past is any guide to the future, that there remain critically important fossils to find, and that the story change when we find them.

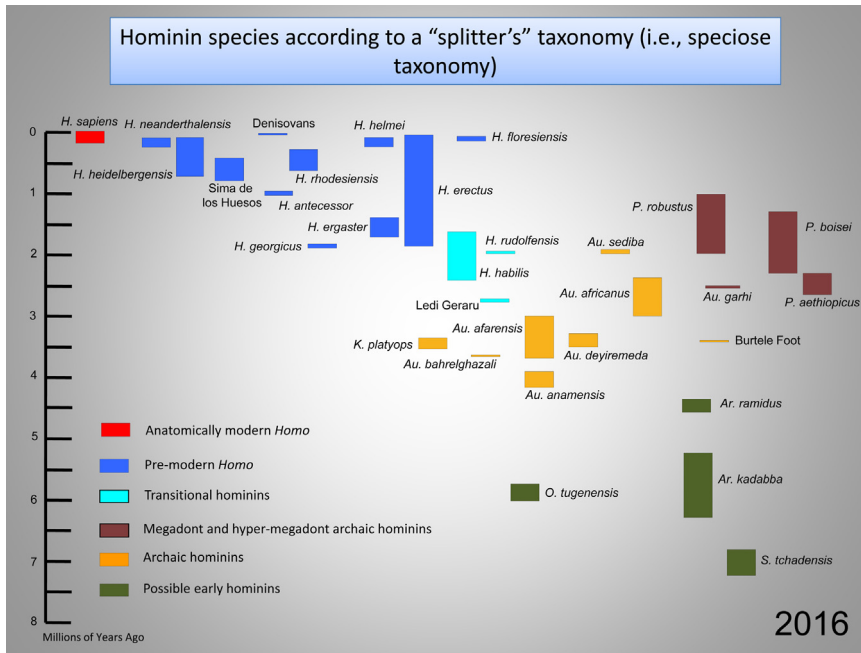


Fig. 1. Hominin species, site collections and individual fossils recognized in a contemporary, speciose, interpretation of the hominin clade. The temporal ranges are conservative estimates. The bottoms and tops of the columns represent, respectively, the most recently published first and last appearances dates. The sources of the data are given in Wood and Boyle (2016).

Fig. 1. Espèces humaines, sites de découverte et fossiles individuels reconnus selon une interprétation contemporaine spécieuse du clade des hominins reconnaissant un grand nombre de taxons. Les intervalles temporels correspondent à des estimations conservatrices. Le bas et le sommet des colonnes représentent respectivement les dates de première et de dernière apparition publiées le plus récemment. Les données sont tirées de Wood et Boyle (2016).

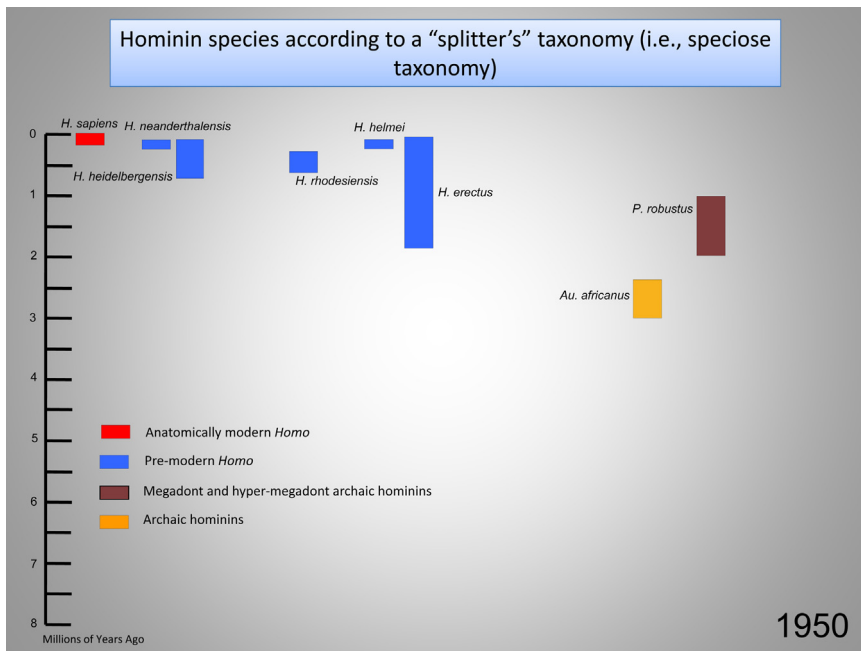


Fig. 2. Hominin species recognized in a speciose interpretation of the hominin clade as of 1950. The bottoms and tops of the columns are the contemporary first and last appearances dates; they do not reflect what was understood in 1950. The sources of the data are given in Wood and Boyle (2016).

Fig. 2. Espèces humaines reconnues dans une interprétation spécieuse de 1950 du clade des hominins reconnaissant un grand nombre de taxons. Le bas et le sommet des colonnes représentent les dates de première et de dernière apparition publiées à cette époque ; celles-ci ne reflètent pas ce qui était compris en 1950. Les données sont tirées de Wood et Boyle (2016).

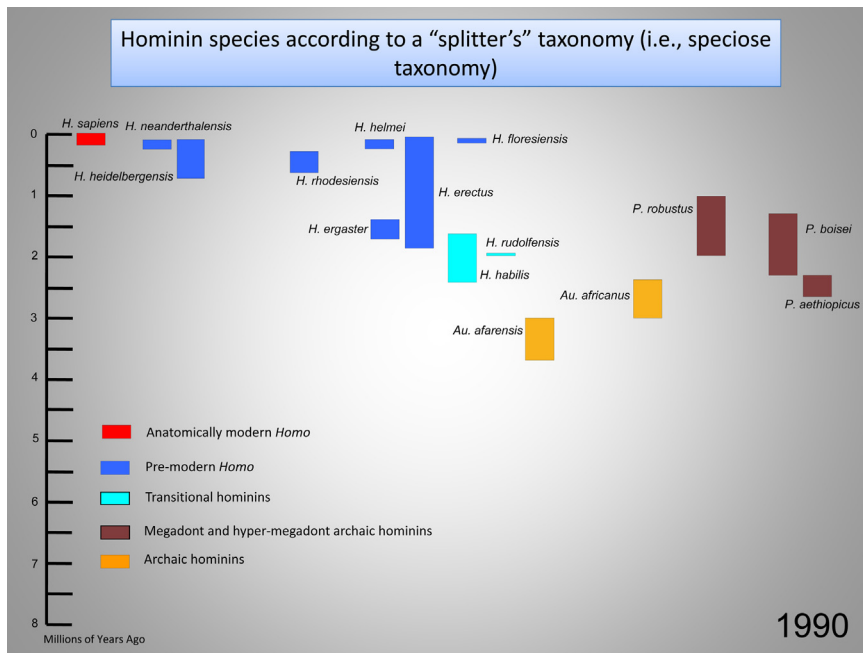


Fig. 3. Hominin species recognized in a speciose interpretation of the hominin clade as of 1990. The bottoms and tops of the columns are the contemporary first and last appearances dates; they do not reflect what was understood in 1990. The sources of the data are given in Wood and Boyle (2016).

Fig. 3. Espèces humaines reconnues dans une interprétation spécieuse de 1990 du clade des homininés reconnaissant un grand nombre de taxons. Le bas et le sommet des colonnes représentent les dates de première et de dernière apparition publiées à cette époque. Les données sont tirées de Wood et Boyle (2016).

Our history is one of disregarding the fact and consequences of unconceived alternatives. We generate comprehensive narratives knowing that we do not have all of the relevant data.

10. Conclusions

When new fossils are published, or new taxa are promulgated, the papers inevitably emphasize the strength of the case being promoted. We fully understand why this is so, but we are also convinced that constructive skepticism may be the most sensible response to many of these claims. In this spirit, in this paper we focus on the types of error that can creep into the analysis of the hominin fossil record when researchers try to answer research questions with data that we believe, for various reasons, are not up to the task.

The task of improving 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, exposes researchers to the temptation to pose, and try to answer, tempting but unrealistic research questions. There is much we would like to know about human evolutionary history, but wanting to know something does not make it knowable.

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Sometimes, and thankfully infrequently, exceptionally talented young scientists are taken from us at the beginning of what had all the hallmarks of being a glittering research

career. Laurent Puymeraul, who had already achieved a great deal before his untimely death, is such a scientist. One can only imagine what he would have achieved if he had lived. It is our sad privilege to offer this contribution in his memory. We thank Andrew Du and Chet Sherwood for their helpful and thought provoking comments on an earlier version of this manuscript. BW is grateful to the GW Provost for support.

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