UNKNOWN BOUNDARIES

EXPLORING HUMAN EVOLUTIONARY STUDIES

An Inaugural Lecture given in the University of Cambridge, 1 February 2005

ROBERT FOLEY

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Exploring Human Evolutionary Studies

The past twenty years have seen a resurgence of interest in human evolution in many aspects. A distinction can be made between 'narrow' (general acceptance that human evolution occurred, historically) and 'broad' (evolutionary ideas that stretch much further into all aspects of humanity, past and present) human evolution. The broad perspective is beginning to make its presence felt, for example, through developments in evolutionary genetics, evolutionary psychology and behavioural ecology. There must therefore be, among the variety of human adaptations, natures and behaviours, phenomena that are not susceptible to an evolutionary analysis, which are beyond the bounds of evolution. The problem is, however, that we do not really know where that boundary lies. Here, the limits of human evolution are explored by using two approaches: first, finding where humans 'fit' the expectations of evolutionary principles; and second, applying evolutionary methods to particular human contexts, while looking for an evolutionary signal. By following this approach not only will the scope and limits of evolution be mapped, but evolution will return as the main framework for anthropology.

ROBERT FOLEY is the Director of the Leverhulme Centre for Human Evolutionary Studies at the University of Cambridge, and Fellow of King's College, Cambridge.

R. A. FOLEY

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UNKNOWN BOUNDARIES: EXPLORING HUMAN EVOLUTIONARY STUDIES

An Inaugural Lecture given by
Professor Robert A. Foley FLS FSA in the University of Cambridge on 1 February 2005

It is almost exactly one hundred years – 1904, to be precise – since the University of Cambridge established a Board of Anthropology. What stimulated a university, renowned then (but not now, of course) for its conservatism, to create such a novel area of study and research, outside the realm of orthodox scientific or humanistic approaches to humanity? One answer, unsatisfactory from the point of view of intellectual history perhaps, but undoubtedly largely correct, is that it came from the determination of some energetic figures at the time.[1] On the one hand there was strong support from powerful figures in the University: Alexander MacAlister, the professor of anatomy, being a key person, William Ridgeway, the then Disney Professor of Archaeology, being another, and James Frazer, the renowned Victorian anthropologist, a third. But above all, there was the figure of A.C. Haddon, zoologist turned anthropologist, and founding father of anthropology at Cambridge (Figure 1). It is clear that his intellectual and practical talents inspired the support of senior Cambridge professors and also, once the Board was established, ensured its success.

Another reason, though, comes from what it was that Haddon and his colleagues were trying to do with anthropology. Again the answer, in terms of many aspects of modern anthropology, will be deeply disappointing. The goal was really to establish the study of anthropology within the natural sciences, to incorporate the natural history of humans into the rest of the biological world. This was anthropology before Malinowski and Boas had become dominant figures and drawn the discipline away from the natural sciences and towards the social ones. Even more, it was the height of evolutionism. The enthusiasts of anthropology at Cambridge saw the subject as an extension of the Darwinian revolution to humanity. Anthropology meant human evolution, learnt through bones, anatomy and fossils, but also seen through the distributions and customs of people. Haddon himself was at the forefront of this work, mounting his pioneering Torres Straits expeditions, and writing extensively on both cultural practices and biological variation.[2]

In 1904, human evolution was the totality of anthropology, including prehistoric archaeology, which came under

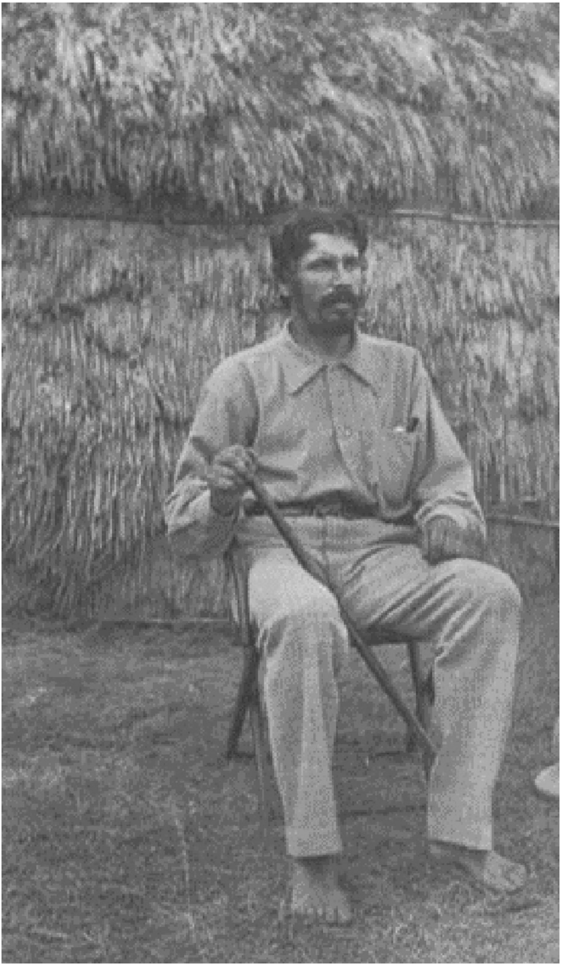

Figure 1. Alfred C. Haddon, founder of anthropology at Cambridge.

the Board of Anthropology. Nothing could be more different a hundred years later. Over the course of the twentieth century this grand view of anthropology as the search for human history through the lens of evolution was abandoned. Social anthropology rejected an evolutionary framework in favour of a purely cultural one. And archaeology – in the words of my Ph.D. supervisor, David Clarke, who died tragically young in 1976 – 'archaeology was archaeology was archaeology', not a branch of any other discipline such as biology or anthropology.[3] And even within physical or biological anthropology the focus gradually drifted away from evolution and more towards human biology and adaptability, as developed in Cambridge by C.G.N. Mascie-Taylor. Certainly, over most of the past century – or at least since the retirement of Haddon – it is hard to see much evolutionary anthropology in Cambridge beyond the fleeting presence of people like Louis Leakey, Phillip Tobias and David Pilbeam. Only in primatology, at the sub-Department of Animal Behaviour at Madingley, was the 'humans in evolutionary context' approach pursued with any vigour, through the work of Robert Hinde, Pat Bateson and a host of distinguished students.

The reason for this shift is clear and has been well documented. The early success of evolutionary biology was like a rapid invasion across many fields of knowledge. But, to continue the military metaphor, the invading forces were only lightly armed with knowledge, and their theoretical bivouacs only flimsily built. The frontier was gradually pushed back, and evolutionary studies retreated to a few easily defended places – the fossil evidence for human evolution, or disease ecology – while in other areas, particularly the nature–nurture debate, prisoners were frequently exchanged and fraternisation occurred. By the second half of the twentieth century, archaeology and anthropology could be said to have the evolution problem well under control – contained, shall we say.

But this is changing now, and this is the theme I want to pursue in this lecture. The past twenty years or so have seen a resurgence of interest in human evolution in all its many aspects. Here I want to make the distinction between 'narrow' and 'broad' human evolution. By 'narrow' I mean the general acceptance of the fact that human evolution occurred, and that in some well-defined topics represents the fully accepted framework, despite the best efforts of so-called creation science, for the long-term history of humans. By 'broad' I mean the view that evolutionary ideas stretch much further into all aspects of humanity, past and present. Here there is less consensus, and often much controversy, but there is little doubt that this broad perspective is beginning to make its presence felt.

Let me give some simple and brief examples. The most obvious one is evolutionary genetics. For the most part the impact of genetics on human evolutionary studies has been seen in the field of phylogenetics: the discovery that humans and chimpanzees are sister clades and remarkably similar, sharing most of their genes; and in the low diversity and recent origin of our own species, *Homo sapiens* (the 'out of Africa' theory).[4] But perhaps far more significant in the long term has been the growing evidence for human genetic variation at particular loci that have major phenotypic effects, especially in behaviour.[5,6] For example, new genetic mechanisms, such as genomic imprinting, are showing that brain functions and cognitive capacities may be under very specific genetic controls, with different parts of the brain, as Barry Keverne has shown, being inherited maternally or paternally.[7] The tools of molecular genetics are exposing the actual mechanisms of human evolution.

Another example would be the rise of evolutionary psychology. Often derided for its popularism – women prefer rich bald old men, which is 67% good news for most male academics – none the less the idea that the human brain is not just a general thinking machine, but rather is a set of adaptations that have been selected for in the context of the particular circumstances in which humans have evolved, has gained wide acceptance and proved a fruitful area of research. This has led to a greater focus on sociality – so often seen as the antithesis of the biological – as a major Darwinian arena, as Nick Humphrey and Robin Dunbar have argued.[8,9] There are also specific hypotheses about, for example, structural differences in male and female brains occurring as a result of different selective pressures, most notably in the work of Simon Baron-Cohen.[10] The functioning human brain, according to this view, is a living testament to evolution.

A third example is behavioural ecology. Ethnographic work has generally been seen as the realm of social anthropology, and well distanced from evolutionary ideas. However, in recent years a strong tradition of ethnographic analysis has been developed by evolutionary ecologists, the results of which are often striking: the work among the Ache of Paraguay, for example, where a whole host of behaviours have been quantitatively demonstrated to be linked to reproductive success. Good hunters, to take one result, are more likely to have more children than poor hunters, both within and outside formal marital relationships.[11]

There are many other fields where evolutionary ideas are encroaching: archaeology,[12,13] economics,[14] medicine.[15] Broad evolution is returning very strongly to the study of humanity.

We can predict, with a high degree of certainty, the responses to this. On the one hand there will be those who say that this is ridiculous, and represents only the return of the myths and errors of the early days of evolutionary anthropology. This was the view of, for example, Edmund Leach, who was emphatic that language marked an impermeable boundary between the evolutionary and the cultural, and that biology in that sense should not intrude into anthropology. The proper study of humans, he said, is the variety of cultures, not the variety of skulls.[16] On the other, there will be those who say that there is nothing off-limits to evolution, and that humanity can be reduced to its nucleotide components. E.O. Wilson not only held this view but managed to upset entire faculties by claiming that, after the triumph of sociobiology, the social sciences would end up as branches of zoology.[17]

I want to suggest here that another response is possible. We all accept that there is a fundamental heritage to humanity that comes from the fact of our evolution; paradoxically, we also accept that humans challenge evolutionary theory in ways that no other animal does. There must therefore be, among the variety of human adaptations, natures and behaviours, phenomena that are not susceptible to an evolutionary analysis, which are beyond the bounds of evolution. The problem is, though, that we do not really know where that boundary lies. Indeed, there are clearly going to be many such boundaries, located at different places and with varying degrees of permeability. Not only do we not know where the boundaries lie, but we do not even know how much they are actually highly dynamic and interactive ones. Hence my title, unknown boundaries.

This, of course, is a bit wishy-washy, a bit 'third way', so I will give you the sting in the tail. There is only one way to find out about these unknown boundaries, and that is to pursue, as explicitly as possible, an evolutionary approach. The relentless march of the life sciences makes it inevitable that we will discover more and more about how humans work biologically, and so by default evolutionary analyses will be extended. However, this is not something that should be left to the molecule-hunters. What is required is that anthropologists and archaeologists engage fully with evolutionary theory and methods in order to determine how humans can simultaneously be both unique and a product of evolutionary processes.

Furthermore, this should not be a philosophical or polemical stance. Exploring the limits of evolutionary biology in relation to humans basically requires empirical work guided by two approaches: first, finding where humans 'fit' the expectations of evolutionary principles; and second, applying evolutionary methods to particular human contexts, and looking for an evolutionary signal.

This is a rapidly emerging paradigm, and one that is leading to institutional support for the interdisciplinary approach that it entails, going beyond the disciplinary boundaries that became established in the twentieth century. In Germany the Max-Planck Society founded the Evolutionary Anthropology Institute in Leipzig. Here in Cambridge, Marta Mirazón Lahr and I, in 2000, proposed the setting up of a Centre for Human Evolutionary Studies at Cambridge, to provide a basis for evolutionary anthropology and archaeology that would bring together the subjects that have traditionally studied humans and their evolution with the emerging fields of the life sciences. The Leverhulme Centre for Human Evolutionary Studies, or LCHES, funded by The Wellcome Trust, The Leverhulme Trust, and HEFCE, represents a major institutional investment on the part of the University, one that reflects the same intellectual pressures that led to the establishment of anthropology one hundred years ago.

The work of LCHES is guided by these two principles: do humans fit the expectations of evolutionary theory, and how well can we apply evolutionary methods to the study of humans? I want to spend the remainder of this lecture exploring these two approaches in the light of the research we are doing.

Perhaps the first place to start is with 'the big picture'. How does the overall evolution of humans compare with how other organisms evolve? The classic view of human evolution has always been that of a ladder of progress, a view so well established that it is a staple cartoon. But is this what we would expect? The rest of the mammalian world tends to evolve not upwards, but outwards. Take any group of animals, and they will usually show an evolutionary pattern that can be described as an adaptive radiation: diversification from a common ancestor. In the iconography of evolution, the pattern is a bush, not a ladder. How does human evolution compare to this? It is a triumph of the traditional field-based approach of archaeology and anthropology that the discovery of more and more fossils has shown that hominin evolution is in fact remarkably bush-like.[18] We now know of about 20 species of hominin – creatures closer to us than to chimpanzees – spread over a period of six million years (Figure 2). And these are not just the older ape-like forms, which might be expected to parallel the evolutionary patterns of other mammals; even in our own genus, with larger brains and technology, there are some ten known species (Figure 3). As at least six of these have been discovered in the past ten years, we have probably not yet reached the limit, and some areas – such as South Asia, where Mike Petraglia of LCHES is discovering new sites – remain relatively unknown.[19]

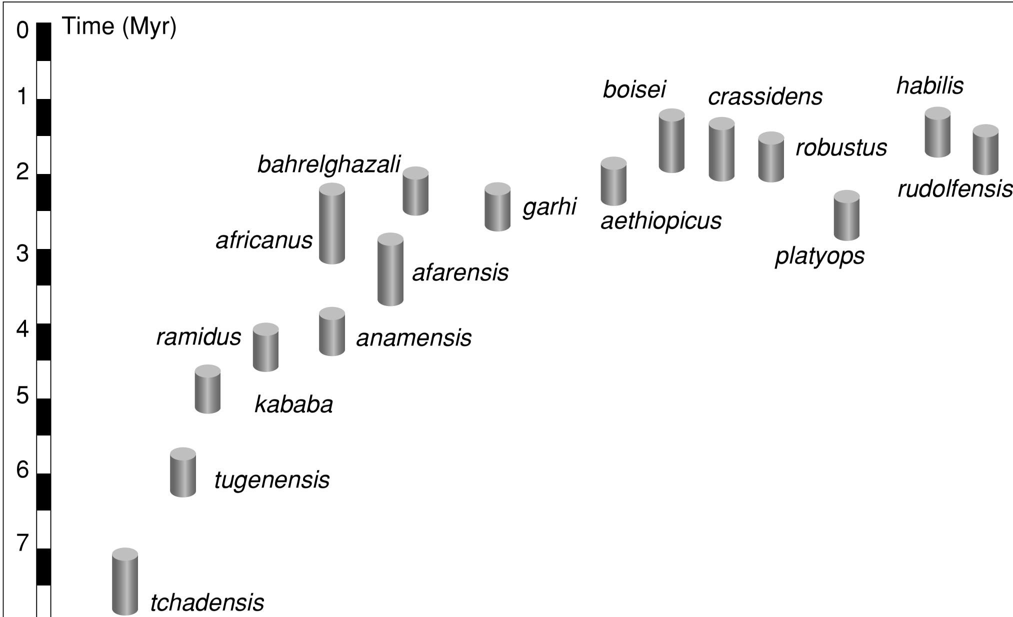

Figure 2. The diversity and chronological distribution of early fossil hominins (excluding the genus *Homo*). Generic names are not shown here. Overall six genera have been recognised for this material (*Sahelanthropus*, *Ororrin*, *Ardipithecus*, *Australopithecus*, *Kenyanthropus* and *Paranthropus*).

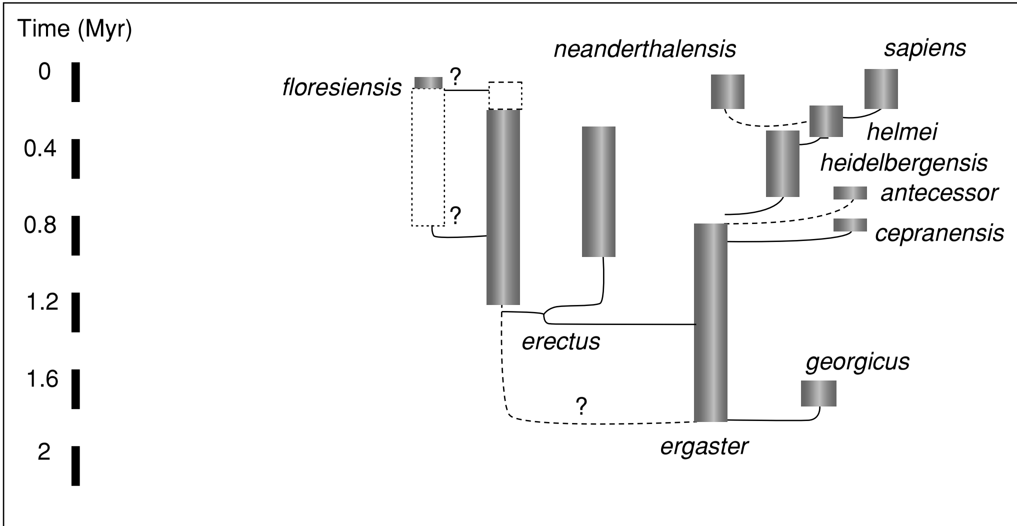

Figure 3. The diversity, chronological distribution and possible phylogeny of the genus *Homo*.

Far from being a ladder of evolutionary progress, human evolution consisted of a series of adaptive radiations, and at virtually all times there has been more than one species of hominin in existence. Even 50 000 years ago, well within the time range of our own species, *Homo sapiens*, there must have been at least three, possibly more. Not only that, but rather than there being a single underlying basis to each of the radiations, it would appear as if each new radiation brought into play another behavioural, cognitive or morphological aspect of human evolution. Human evolution was not triggered by a single spectacular novelty, but by the accumulation of many over a long period of time, each one leading to speciation and diversity; only very recently has the lineage become reduced to a single, globally dominant species.

If the pattern of human evolution is remarkably like that of a typical mammal, what of the processes? This gives me a chance to mention what is perhaps the most spectacular of recent discoveries: *Homo floresiensis*.[20] Unlike most finds that catch the world's attention, this one is important not because it is so old, but because it is so young, only 18 000 years.

However, it is another aspect of this species that I think throws light on the way human evolution fits the expectations of evolutionary theory in terms of process. Peter Brown and colleagues described the fossil as a pygmy

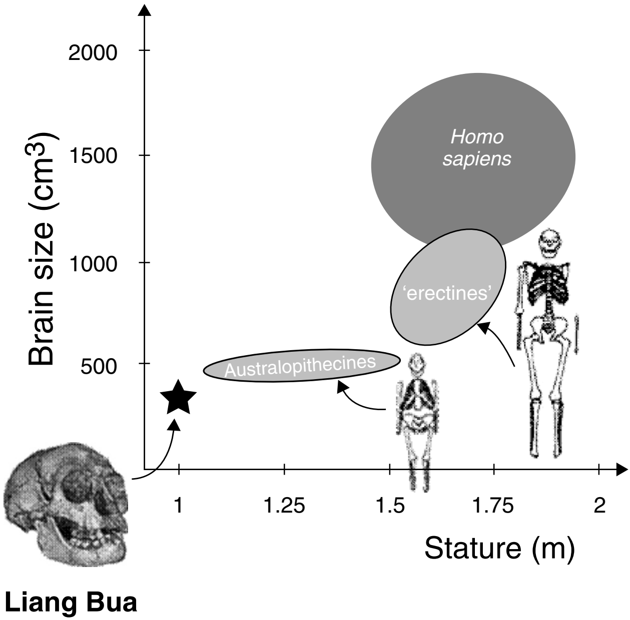

Figure 4. Body size and brain size relations of the hominins, showing the position of the new specimen from Liang Bua, Flores, assigned to *Homo floresiensis*. This is the most extreme hominin known in both brain and body size.

version of *Homo erectus*, sufficiently different to be a new species (Figure 4). Standing at around one metre in height, it is probably among the smallest human-like creatures ever. As Brown pointed out, it is the context of this that makes this diminutive size so interesting: it was isolated on an island. Island dwarfism is a well-known phenomenon, with pygmy elephants and pygmy deer found on many Mediterranean and other islands.[21] Humans, or human-like creatures, were not immune from this process. Limited resources, unique mortality patterns, and lack of predators account for this phenomenon across many species – on islands it seems best to be about the size of a goat! – and human-like creatures were no exception. Even late in our evolutionary history it seems that culture did not buffer our lineage from the normal processes of island endemism.

These pygmy hominins perhaps provide another insight into human evolution, one that emphasises that this is classic natural selection at work. Simon Conway Morris has often argued that the best evidence for Darwinian evolution is the widespread occurrence of convergence or homoplasy (the same thing evolving in more than one lineage).[22] There is plenty of evidence for convergence across the whole of human evolution,[23] and *Homo floresiensis* is yet further confirmation of this. Human pygmies occur in what can generally be considered forest islands; furthermore, the genetic evidence strongly suggests that several populations in Africa, Asia and South America have evolved pygmy characteristics independently.[24] The little hominin of Flores suggests that this trend occurred among other lineages, subject to the same selective pressures, prior to modern humans.

The pattern of hominin evolution, and even discoveries such as the Flores hominin, would seem to fit the expectations of evolutionary biology, and provide a useful example of how we should be using evolutionary principles to test the usefulness of this approach. So far, so good, would seem to be the result at this point. However, it would be unreasonable – if tempting – not to mention an aspect of *Homo floresiensis* that was not entirely expected. Not only is this species very small, but it also has a very small brain, smaller than that of any known hominin, 380 cm^3 compared with modern humans (1400 cm^3). Estimates of its degree of encephalisation based on its body size would still place it within the range of the australopithecines. Its brain is smaller than that of its putative ancestor, suggesting an actual decrease in size during the course of its evolution.

Is this surprise a problem for an evolutionary approach? Certainly there is nothing in evolutionary biology to rule out reversals, even for brain size. Early modern humans, for example, in many cases have larger brain sizes than are found in some contemporary populations.[25] What is a challenge is to identify the conditions under which reduction is advantageous. Less social complexity? Changed patterns of growth under restricted resource availability? At the moment, it is difficult to say, but this discovery provides an example where the expectations of evolutionary theory are far from clear, and human evolution can contribute to its development.

Pygmies – this time modern ones – allow us to explore another area where we can see whether humans fit the expectations of evolutionary theory. Exceptionally small body size has long been of interest to anthropologists, and explanations for it have ranged from heat adaptation, to reduced nutritional availability, to mobility (moving in heavily forested environments).[26] Each of these may contribute to the answer, but recent developments in life-history theory may yet provide us with a more theoretically satisfactory explanation. Life-history theory predicts that patterns of growth and ageing are shaped by trade-offs between energetic demands from growth and reproduction, and that these are strongly controlled by survivorship. Current research at LCHES by Andrea Migliano and Marta Mirazón Lahr, has shown how these theoretical predictions can explain pygmy stature in populations of high adult mortality, compromising pubertal growth in order to reproduce earlier.[26] The costs of late reproduction – given the high chances of dying – are too great for them to be able to afford the luxury of a large body size. This pygmy extreme has a mirror among other populations where adult mortality is lower, body size is larger and age of first reproduction is much later. This life-history approach not only shows the continuity between the evolutionary biology of contemporary and fossil hominins, but also has the potential of explaining how something as extreme as *Homo floresiensis* may have been adaptive.

Here we are at the heart of what evolutionary theory can do for anthropology. By taking broader models that focus on the key parameters of Darwinism – reproduction and mortality – we can see how something as fundamental as the size and shape of humans is the product of selection. At the Centre, Lucio Vinicius is now extending these models to determine how they might also explain longer-term patterns of human evolution.[27] And what is more, we know that when you first reproduce is among the most critical transformations in any human community – often marked socially – and so this chain, from mortality to growth to reproduction, will have ramifications far beyond the purely biological.

It could be argued that so far I have carefully chosen examples that are close to the heart of what evolutionary biology is about, namely speciation, growth, development, size and brains. What, you may ask, about things more cultural, less obviously biological? Here it is more difficult, if only because it is less clear what the expectations might be. We can start by taking one aspect of culture as a human property: the tendency of human communities to form units that share behavioural, social and

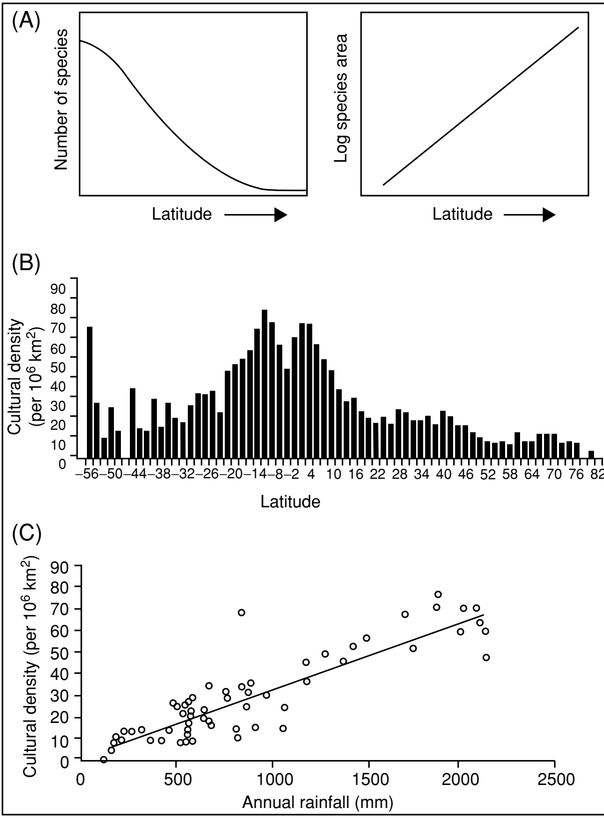

Figure 5. Biogeography of human cultures. Ecologists have shown that there is a strong pattern of diversity and species area with latitude (A). Human cultures show a very similar pattern (B); the diversity of human culture in any region can be predicted on the basis of rainfall and temperature data (covaries with latitude)(C). (Modified from reference 29).

linguistic traits, and differ from other such communities – cultures, in other words, rather than culture.

In animal biogeography there is a well-known phenomenon known as the latitudinal gradient: there are more species per unit area close to the equator, and this declines with increased latitude.[28] Species diversity is greater in the tropics (Figure 5A). Another way of putting it is that species at higher latitudes have greater geographical ranges than species at lower latitudes. Although there has been considerable debate as to what causes this gradient, there is general acceptance that it occurs. What happens when we consider human cultures in the context of these expectations? The answer is that they follow much the same pattern (Figure 5B). It turns out that the number of cultures per million square kilometres is very predictable. More specifically, we can write an equation that very precisely accounts for the number of cultures in terms of rainfall and temperature (Figure 5C). These analyses are at a global scale, and it could be argued that this scale hides the messy noise of human variation, but if we repeat the analyses for different longitudinal bands, the results remain much the same.[29]

What does this tell us? Not, I would be the first to say, that human cultures are just like biological species. But we can say a number of things. First, that approaching a meaningless set of dots on a map – the distribution of cultures in this case – with a hypothesis and quantification can lead to interesting results. Second, that there is clearly an important underlying ecological – and hence potentially evolutionary – basis for cultural diversity. If we ask what is happening when separate cultures form, we can say that there is a tendency for groups to build boundaries between each other (even if they are permeable) and that this is environmentally conditioned – most probably through levels of inter-group competition and interaction, but possibly deriving out of even more micro-scale processes such as marital patterns, which in turn will reflect resource distribution.[30] This means that even something as apparently uniquely human as our tendency to speak different languages is part of an evolutionary process. That this will feed into other aspects of our diversity – for genes often follow languages – is a reason for seeing the cultural pattern of human diversity as part of a larger picture, one shaped by evolutionary processes.

In analysing human cultural diversity we looked at something that would initially seem to be beyond the bounds of evolutionary theory, but in practice conformed to some fairly standard ideas in evolutionary ecology and geography. This is evolutionary biology helping because there is an appropriate model, which not only makes the right empirical predictions, but also provides the basis for an explanation for how and why human communities form and are maintained.

What happens, though, when the evolutionary expectations come not from a well formulated theory, but from some empirical observations? To illustrate this I want to turn briefly to the genetics of modern human evolution. Nearly everyone is now familiar with the idea that modern humans have a recent origin in Africa. By recent, I mean about 150 000 to 200 000 years ago. Much of the impetus for this model has come from genetics, and the fact that human diversity is very low compared to that of apes, and that the highest level of diversity is to be found among African populations, diversity in the relevant genetic systems being largely a function of time.[31] Although this came as a bit of a surprise – and still does to some people in the field – it is not really that dramatic, as humans had to evolve somewhere and sometime, and this fits many other lines of evidence.[32,33] There is, however, another element of the genetic data that is truly surprising in the context of generally held anthropological and archaeological ideas, namely that the ancestral population in Africa from which we are all derived was remarkably small: no more than 50 000 people, and probably considerably fewer.[34]

Why is it a surprise? I think partly because anthropologists had on the whole not given a great deal of thought to actual population sizes among early hominins, not least because it seemed impossible to know. Another reason, though, was that it was assumed that over the course of human evolution there has been a gradual increase of population, culminating in the sorts of demographic pressures that led to the development of agriculture some 10 000 years ago. Underlying anthropology and archaeology has for many years been the idea of humans as a demographically substantial and resilient species. However, evolutionary genetics has thrown an entirely new light on human prehistory with which we are still coming to terms: that human prehistoric populations were in a state of repeated flux and fragility. Rather than being buffered by their culture and technology, they were still very much subject to the oscillations of climate, to the point where at times – during the frequent extremely cold and arid phases that characterise the climate of the last million years – hominin populations may have been very sparse and scattered, isolated to a degree that is now unimaginable.[35]

How does this serve to make us think about humans in an evolutionary light in ways we did not previously, and thus help us with our unknown boundaries? In two ways. First, if for much of our recent evolutionary history we were indeed made up of small populations, then we are likely to have been hotbeds of evolution. Ever since R.A.

Fisher developed the mathematical principles of natural selection here, we have known that evolutionary change – through both selection and drift – is more likely to have occurred in smaller rather than in larger populations. This helps us to understand the growing diversity and apparent chaos of much of what is known in the fossil record. Second, and more importantly, we are for the first time turning to a new question in human evolution that has received very little attention, namely extinction. Far from our being the ultimately successful lineage, extinction of small populations now seems to recur throughout the record. We are familiar with the idea of the Neanderthals becoming extinct, and now *Homo floresiensis*, but – as Marta Mirazón Lahr has shown through her studies of human cranial diversity over the past 100 000 years – many modern human populations also became extinct. In many parts of the world, we can see one population disappear abruptly, and another appear.[36]

Extinction, then, is not something that just happens to other species: it is an important part of our evolutionary heritage. We are just beginning, at LCHES and elsewhere, to focus on this issue, through studying demography in declining hunter–gatherer populations in the Philippines and elsewhere, through genetics, and through the archaeological record. However, although this has been something of an anthropological surprise, it will come as no such thing to most palaeontologists. Again, evolutionary theory should have led us to see extinction as an essential part of human evolutionary history; it was perhaps our anthropological blinkers that prevented us from doing so until we had to grapple with the new genetic evidence.

I said earlier that we can search for the boundaries of evolutionary biology in two ways. First by seeing how human traits and patterns fit into the expectations of evolutionary theory. As we have seen, they generally do, although this does not rule out that they might not fit other models as well. And there is no reason why this approach cannot be extended to other spheres: religion, perhaps, as Pascal Boyer[37] and Robert Hinde[38] have done, or kinship. However, what we have shown here at least provides us with a basis for saying that this approach does have the potential for mapping human evolution and its ramifications today. The second approach is more heuristic: applying evolutionary methods to particular empirical problems, and finding out whether they identify an evolutionary signal or not.

The evolutionary signal I have in mind can be thought of in two ways. First, evolution can be considered – and indeed was originally described in this way by Darwin – as descent with modification. Put another way, this means that evolutionary products can display a tree-like structure in their relatedness. This, of course, is and has long been the core of much work in evolutionary biology, including anthropology. It has recently been greatly extended and enhanced both by the growth of molecular techniques and by the use of a cladistic methodology. It is the fact that we can demonstrate fairly clearly the relatedness of genes that has allowed us to reconstruct the history of recent human populations fairly precisely. The question is, what else can we demonstrate to have the tree-like structure we associate with evolution?

An obvious place to start is with skulls. Human morphology has long been used to reconstruct phylogeny, and indeed was the basis for most of the earlier work on human evolution and diversity. There were, after all, few other sources of data. Much of this work fell into disrepute, but this is a reviving field. It is probably true that little can be learnt from simple measurements of lengths and breadths of skulls, but a great deal can be learnt from the complex three-dimensional morphometrics that are now possible, and which take into account environmental or biomechanical adaptations, such as those being developed by Jay Stock at the Centre. Broadly speaking, these results show something similar to the genetics: that African variation is greater than that elsewhere in the world. The pattern is far from identical, raising all sorts of interesting questions about the relationship between genotype and phenotype, and the scale of variation, but none the less supports the idea of a complex and ancient population history in Africa. Moreover, phylogenetic analysis of fossil crania supports the patterns of extinction discussed earlier and suggests that some human populations, nested within living ones, did become extinct, and that the distribution of modern human populations in Africa has changed radically over the past twenty millennia or so.

It is satisfying that there is a phylogenetic signal to the human phenotype that matches the genetics. Matching the two may become even more interesting once ancient DNA, an area the Centre is developing, becomes more widespread and allows us to compare genotype and phenotype across time. However, some would say that looking for a phylogenetic signal among skulls is hardly a major challenge. The real question is whether we can see this phylogenetic signal in other, less obviously biological, traits. That will be the test of whether evolutionary approaches are likely to reach all parts of archaeology and anthropology.

One such area is stone tools, an area of study in which Cambridge has had many distinguished contributors, from Miles Burkitt to Charles McBurney to Paul Mellars. Stone tools make up the richest part of our evolutionary past and extend the human fossil record beyond the morphological to the behavioural. Variation in technology in the Pleistocene has generally been considered to be adaptive, flexible, and subject to local contingency and choice by hominins. As such, it should vary in relation to the environment. However, it has become increasingly clear that, although there is some local environmental variation, in practice the major technological modes are remarkably widespread, stable over long periods of time, and often disappear and appear abruptly.[39] In pattern, they do not look as if this is technology as we know it today: endlessly adaptable and changeable in relation to need. A long time ago we upset a lot of archaeologists by asking what happened if we used evolutionary and cladistic techniques to build phylogenies of tools, as if they were fossils.[40] When we did this, it turned out that there was a remarkable congruence between the two. Technology displays much the same phylogenetic signal as the hominin fossils (Figure 6).[41] This is not the place to go into the details of this, but rather to emphasise a different point. Once we start to treat stone tools – the archaeological record of the Pleistocene – in the same framework as the fossils, not only are we reminded that they are all part and parcel of the same evolutionary history, but we can ask new questions about the relationship between behaviour and biological evolution: which comes first, is there a pattern? When does behavioural change correlate with speciation?

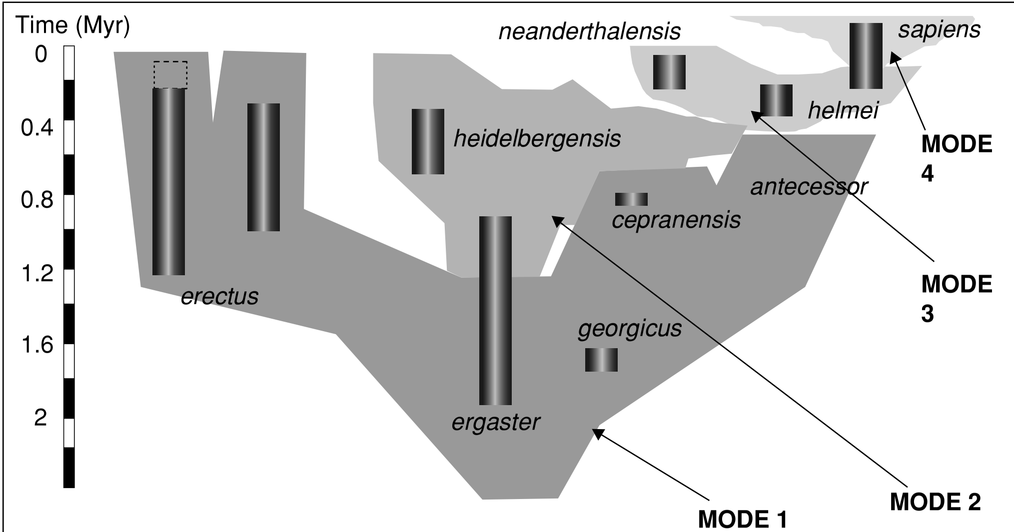

Figure 6. The phylogeny of stone technology in early prehistory. The columns show the distribution of hominin taxa. Superimposed on these are the shaded polygons that reflect the distribution of major technological modes. Mode 1, pebble core and chopper industries (e.g. Oldowan); Mode 2, bifaces (Acheulean); Mode 3, prepared core technologies (Middle Palaeolithic, Middle Stone Age, etc.); Mode 4, blade technologies.

The opportunities are endless, and we are pursuing these at different scales. One project is in fact returning to some very old work of Haddon, who provided a detailed description of canoe technology in Melanesia, and using this to look for a phylogenetic signal among the recent populations of the region.

Cladistics is proving to be a powerful tool for exploring hypotheses in evolution, and there is no reason why it should not become so in archaeology and anthropology. It may also provide a means of solving problems in other areas of the subject.

Since 2002 we have been involved in a large European collaborative research project called the Pioneers of Island Melanesia, co-directed by Stephen Levinson, of the Max-Planck Institute for Psycholinguistics at Nijmegen, and myself. In a way it epitomises what I have been talking about in this lecture: interdisciplinary approaches, within an evolutionary framework, to particular anthropological problems. The project involves geneticists, archaeologists, anthropologists and linguists. In this case the focus of our work is the diversity of the languages in the area, and how this came about. There are numerous languages, falling into two groups: Austronesian, which are a set of closely related languages, and non-Austronesian, or 'East Papuan', which are highly diverse and isolated one from another. The general expectation is that the Papuan languages represent the older layer of human populations, whereas the Austronesian-speakers came more recently, probably with the makers of Lapita pottery.[42]

The problem for the linguists is that the languages are so different one from another that they have proved intractable to traditional approaches based on cognates. In Colin Renfrew's terms, they are a classic example of whether there is a limit to how far back we can go to reconstruct linguistic history.[43] This is currently assumed to be about 8000 years, but the Papuan languages are thought to have diverged earlier than this. To solve this problem, we have been experimenting with biological techniques designed to extract a phylogenetic signal. Michael Dunn, Angela Terrill and Ger Reesink, of the Max-Planck Institute in Nijmegen, have constructed a database of grammatical structures for the Melanesian languages. The hypothesis is that grammar is more stable than vocabulary and will therefore retain a phylogenetic signal longer. We have then used cladistic algorithms to explore the phylogeny. We found that the method could replicate the well-known Austronesian language phylogeny based on vocabulary. The question was, would it pick up any signal among the Papuan languages?

I think it is fair to say that it was much to the linguists' surprise that it did. Although all these Papuan languages share no borders with each other, and are often widely separated, none the less the best trees turned out to follow the geography very closely. The major branches on the cladogram of the Papuan languages represented the three significant island groups: the Bismarcks, Bougainville, and the Solomon Islands.[44]

I should point out that it was not the primary aim of this project to use evolutionary techniques to build linguistic history, but it has proved to be an interesting exercise. Indeed, perhaps what is striking is that there is in fact a much clearer geographically based phylogenetic signal for the languages than for the genes. This is very exciting, for this is what the project is really about – and this takes us back to our earlier discussion of cultural diversity – what leads human communities to form boundaries, and how different aspects relate to those boundaries: genes, languages, technology. Island Melanesia is a microcosm – an evolutionary laboratory – for all the larger issues that I have been discussing this evening.

These examples have been about using evolutionary methods to identify descent with modification, and thus patterns that suggest something much like an evolutionary process underlies our history. And, of course, it is history that we are talking about here: changes in human populations and communities over time, which indicate at least a concordance with how evolution works and hence suggests that there is a value in using this approach. But what exactly is it we are proposing here as an evolutionary mechanism? Surely it is not genes for speaking a particular Papuan language under a selective regime. Obviously not, although it is very tempting to suggest that there is a strong genetic component in hand-axe manufacture among widespread populations over a million years or so. The sort of model one has in mind is one of cultural evolution as proposed by Boyd and Richerson,[45] in which there are a series of mechanisms that give traits – languages, technology, artistic symbols – adaptive value to the populations. Exactly what those traits are may sometimes be highly significant – a better way of making a canoe – and sometimes entirely arbitrary – a particular word for canoe – but provide an advantage due to context (everyone uses the same word to describe a canoe, or everyone has the same tattoo). The point is that they are traits possessed by individuals in a group context, which gives both the individual and also the group an advantage. It is the success of the latter (the group), spreading the distribution of the descendants of the former (the individual), that leads to this phylogenetic signal of cultures, and the fact that new groups essentially form through the divergence of existing groups, hence the diversity of groups and cultures; and of course, as we saw earlier this occurs, at a higher rate in low latitudes compared with high latitudes.

Of course we know too that new communities can be formed not only through this process of bifurcating ethnogenesis, but also by fusion, absorption and so on.[46] And here we come to the crux of the matter. If cultures show a phylogenetic signal, a branching pattern of descent with modification much like I have shown, then we have gained insights into the process of change; equally, if there is only a very weak phylogenetic signal, then we can draw a different set of inferences. The point I would stress is that evolutionary methods provide the means for distinguishing between them; they provide a technique for mapping the boundaries, rather than assuming we know where they lie.

If the techniques for looking for descent with modification – looking for a tree structure – are a powerful means of charting the territory of human evolutionary studies, they are perhaps still not sufficient. Why not? They are not sufficient on their own because while they show us that something 'evolutionary' has been going on, we do not know whether the processes are indeed Darwinian – that is, whether they involve selection and adaptation. But, when we look back at how life history among the pygmies reflected mortality and reproduction, and how this influences the ebb and flow of cultures, we can see that there is every reason to see selection and adaptation as playing a major role in having shaped the processes of descent with modification. The hands of Darwin and Wallace lie behind this emerging, multidisciplinary anthropology and archaeology, and in the end will form the heart of the new evolutionary anthropology that is emerging.

This lecture began by looking back to the beginnings of the Board of Anthropology and Archaeology in Cambridge, at a time when evolutionary approaches to the study of humanity were almost so obvious that they were hardly ever made explicit, and where the boundaries between what are now biological and social anthropology, and between them and prehistoric archaeology, did not exist. All were united by a common framework involving history and adaptation – what we would now call phylogeny and selection.

Today, we take a very different view, with institutions firmly established which define exactly where the boundaries between our understanding of humanity – culture versus biology – lie. More and more, the frontiers between different elements of knowledge also coincide with administrative and resource-based units, thus making the boundaries not just vague lines on maps of knowledge deserts, but strong fortifications. At present these fortifications define what I have referred to as the ‘narrow’ view of human evolution. In establishing the Centre for Human Evolutionary Studies it is our hope that in Cambridge and elsewhere we will embrace the broader view. The interdisciplinary approaches, going far beyond archaeology and anthropology, but involving genetics, medicine, zoology and psychology, are the way forward if we are going to go some way towards mapping what I have referred to here as the unknown boundaries between what is evolutionary, and what is not. And, of course, in the end determining what are the implications when we discover the answer.

In making the case for a broader approach to evolution, rather than a narrow one, I am not starting a new debate. When anthropology was founded at Cambridge, it was not Haddon who was first appointed, and it was not in Zoology, where the support for the natural-history perspective of humans was strongest. Haddon was – like a good anthropologist – away in the field, in the Torres Straits, when the appointment became available. It went instead to Wilfred Duckworth – after whom our biological collections are named – and it was in Anatomy, rather than Zoology. Duckworth went on to make major contributions, but not on the scale and breadth of Haddon, who was eventually given an appointment. Both Duckworth and Haddon were evolutionary anthropologists, but perhaps I am not alone in thinking that the breadth of Haddon's approach to human evolutionary history is what is needed if we are going to develop a more integrated and coherent view of ourselves.

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