

Structure and Contingency

Evolutionary Processes in Life and
Human Society

Edited by

John Bintliff



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Contents

Contributors	vi
Preface	vii
Introduction: The scales of contingency and punctuation in history <i>Stephen Jay Gould</i>	ix
1 Selection and the fossil record <i>Chris Paul</i>	1
2 Evolution and environmental controls: Palaeozoic Black Deaths <i>Michael House</i>	14
3 Pattern and process in hominid evolution <i>Rob Foley</i>	31
4 Contingency, patterning and species in hominid evolution <i>Alan Bilsborough</i>	43
5 The human evolutionary time-scale and the transition between hunting and gathering, and farming <i>Robert Layton</i>	102
6 History, ecology, contingency, sustainability <i>I. G. Simmons</i>	118
7 Structure, contingency, narrative and timelessness <i>John Bintliff</i>	132
Index	149

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Preface

The theme of this edited volume is the appropriate methodology in which the history of life on earth may be examined and understood, in particular, the interplay between form and structure – the things that we might predict and model, and those things that we cannot predict, we can only ‘postdict’ – the arbitrary, the contingent, which may be as important or even more important to the way in which *life on earth and human history have evolved*. I have selected a group of palaeontologists, human evolutionary specialists, an anthropologist, a human palaeoecologist and an archaeologist to address this theme: the time-scales covered commence with the development of life on earth, move on through human evolution and then into the very modest time-scale of later prehistory and historic archaeology. Essential to our interest in this theme have been the writings of Professor Stephen Jay Gould of Harvard University, who has developed a distinctive philosophy of history concerning the nature of long-term and short-term evolutionary processes, particularly stressing the interplay between structure and contingency. I am delighted that Professor Gould has written an introduction to the volume.

John Bintliff

Contents Preface

The first part of the book is devoted to a general introduction to the subject of the book. It is divided into two chapters. The first chapter is devoted to a general introduction to the subject of the book. The second chapter is devoted to a general introduction to the subject of the book.

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Introduction: The scales of contingency and punctuation in history

Stephen Jay Gould

The range and power of narrative style in science

Our fascination with history lies in the appeal and interplay of both opposing themes in Karl Marx's famous opening comment to his *Eighteenth Brumaire of Louis Bonaparte*: 'Men make their own history, but they do not make it just as they please.' The second phrase – 'not ... as they please' – stresses the timeless and the predictable in universal structure, the necessary lawfulness of nature that human caprice cannot alter. And upon this rock (of stability), we build much of our hope for making sense of a world that often seems so arbitrary and so complexly unknowable. But the first phrase – 'men make their own history' – acknowledges the potential import and meaningfulness of our individual lives, the promise that our personal actions and struggles can budge (or even redirect) the apparent indifference and inertia of external reality. And upon this hope (of mattering), we build much of our courage to face the Rock of Ages.

The strongest version of the ahistorical model (truly atemporal as well, at least in denying uniqueness or distinction to particular

moments) resides in a cultural stereotype attached to the physical sciences (often with some justification, and with substantial approbation of practitioners). In the simplistic version, taught to schoolchildren as *'the scientific method'*, researchers attempt to remove all distinctiveness of time or place by reducing the overt complexity of a natural phenomenon to a few repeatable and controllable factors, bringing this reduced system into the laboratory (or controlling the situation adequately in the field), perturbing the simplified system by recorded and quantifiable changes in one or a few variables, measuring the outcome, and repeating the procedure with adequate control to assure the same results. In other words, simplification, generalization, control, quantification, and replication. In ideal circumstances, we learn how nature's spatiotemporally invariant laws operate to yield predictable results from specified initial conditions. Explanation may be the final goal, but success in prediction stands as a primary validation (while positivist philosophy has long held, in any case, that explanation and prediction are logically symmetrical – and only psychologically distinct by the accident of past or future occurrence, an irrelevancy in a universe of temporally invariant laws).

This method can be so powerful (when we find appropriate material for its application), and the prestige of physical science has risen so high as a result, that historians often become beguiled, and seek to apply the same apparatus to their own disparate and inappropriate data – a mistaken procedure that some commentators have justly described as *'physics envy'*. Thus, for example, historians from Spengler to Toynbee have tried to find predictable (if not quantifiable) and repetitive cyclicality as a *'scientific'* bedrock for vagaries of history that then become *'mere'* particulars in any given rerun of a basically determined process.

But many scientists, particularly those (like myself) who work in fields charged with trying to understand the definitive events of complex historical sequences that can occur but once in all their detailed glory (the extinction of dinosaurs for palaeontologists, the origin of the earth's single large moon for cosmologists, the evolution of human intelligence for anthropologists), cannot use this apparatus of timeless generalization to explain their key phenomena. (The physics of impact will surely help me to understand what a large bolide might do to earthly climates, but a full explanation for the extinction of dinosaurs requires a knowledge of numerous particulars, not just a grasp of the physics of a triggering cause).

Historical scientists – and I stress the word *'scientist'*, for they are of the same ilk, while following another style appropriate to their

distinctive material – recognize that they must apply a different, narrative method in pursuit of the major goal common to all science: rational and falsifiable explanation of natural phenomena in a manner that can lead to general understanding (not just a mere account of particulars) by applying the same apparatus to similar problems in widely varying contexts. Narrative explanations do not follow deductively from nature's laws (though, needless to say, they do not and cannot contradict any genuine and general atemporal principle). They require a knowledge and reconstruction of actual sequences of antecedent events, for outcomes are contingent upon a previous chain of occurrences, each of which could have unfolded in a different way (and sent history cascading down a disparate channel) if we could rerun the sequence from an identical starting point (the great undoable *Gedanken* experiment). Narrative explanations may be as detailed, as decisive, and as satisfying as anything learned by the experimental method, but they do not permit prediction from a known starting point – and the venerable claim about symmetry between prediction and explanation in science is therefore false as a universal principle.

This unusual and interdisciplinary book explores the role of narrative, contingency-based explanations in historical science across the full range of scales for the study of life, from the most general features of the fossil record in Darwinian evolution of life at geological scales measured in billions of years (Chapters 1–2) to principles of cultural change over hundreds of years in the single species *Homo sapiens* (Chapters 5–7), with an intermediate scale for hominid evolution during the few million years of our own lineage's existence (Chapters 3–4). The narrative style featured in this book seems congenial, insightful and appropriate for two major reasons, one of the external world and the other of human psychology. First, the nature of history's complex and singular unfoldings enjoins this style of explanation as the only adequate approach for achieving the detail of understanding that we seek. Second, the mentality of *Homo sapiens* seems to favour the story-telling mode, so we should not eschew such a natural inclination when we utilize material appropriate for our best skills.

At the same time, we must be especially wary of accepting explanations that tickle the fancy of our preconceptions – and we must therefore recognize that humans not only favour the narrative mode, but that we like our stories to 'go' in certain ways (at least as a legacy of Western cultural traditions). We especially like stories about growth and progress (or the obverse tragedies of death and destruction) based on the meaningful intentions and struggles of heroic actors. This predilection leads to our penchant for predictable

progress as an organizing principle for the history of life and human culture – a penchant all the more abetted by the consonance of such narratives with the favoured themes of prestigious experimental science: prediction and replication. Therefore, while defending narrative as an appropriate style for many kinds of scientific investigation, we must be suspicious of our cultural and psychological preferences for certain sorts of stories. This book focuses on narratives that question these biases by stressing the distinctive motifs of raw history: chance, uniqueness, unpredictability, and crucial episodes of major and unexpected change – in short, the dominant themes of contingency. If we can introduce to science both the unfamiliar style of narrative explanation, and then also champion a set of uncongenial themes in the history of Western narratives, then we may be performing a service in expanding the modalities of legitimate scientific inquiry.

To illustrate how well this book succeeds in both these worthy endeavours, I will use the chapters herein to illustrate two constellations of themes that have been central to my own view of how a general philosophy of narrative science might be articulated and applied: the meaning and power of contingency itself, and the relationship between punctuational models of change and the quest for a science of historical sequences.

The appeal and status of explanation by contingency

Contingency has been seriously undervalued (even actively rejected) as a mode of explanation because its style of argument falls on the wrong side of one of our worst mental errors – our lamentable tendency to treat complex issues by dichotomizing choices into 'either' *vs* 'or'. This mental taxonomy, false enough as a logical failing, then becomes even more unfortunate when we follow another human propensity and grant moral weight to our imposed divisions – so that one choice (the one we favour of course) becomes 'good', and the other 'bad'.

(Nature, to be sure, does present us with some outstanding and reasonably objective divisions by two – night and day for each earthly rotation, male and female for the coupling that gives us evolutionary continuity, for example. But we so often force dichotomous division upon richer and clearly inappropriate complexities – liberal or conservative, God-fearing or atheistic – that I tend to side with Lévi-Strauss and his Structuralist school in regarding dichotomization as a universal, evolved, and distinctly suboptimal strategy deeply built into our biological nature. This evolutionary 'error' becomes all the more unfortunate when, in our

granting of moral weights, we anathematize, punish, or even murder the folks of opposite persuasion.)

Contingency has been stigmatized by conflation with the 'wrong' end of a classic (in false construction) and improper (in moral weighting) dichotomy: determined and predictable *vs* random and chaotic (with both descriptors of the latter and 'wrong' end used in their vernacular rather than their quite different scientific senses). Under this scheme, some outcomes are determined by laws of nature operating upon a given set of initial conditions. These results are predictable, therefore 'scientific' and 'good'. Under the thrall of our mental dichotomy, other outcomes that are not predictable must therefore be 'random' – meaning, in everyday English usage, unexplainable, literally senseless, confusing, and altogether unfortunate, not to mention unscientific.

Contingently conditioned outcomes get the short end of this particular stick. Once we acknowledge their unpredictability in principle, we relegate them without further ado to the 'bad' category of random (meaning inexplicable). We therefore miss their most intriguing characteristic – the property that makes them the 'flagship' outcome for the different, narrative style of scientific conclusion: that is, their tractability for fully satisfying explanation after the fact, despite their inaccessibility to prediction from a known starting point.

At the very best, we might grasp that contingent does mean explainable (by sequences of antecedent occurrences rather than by prediction from laws of nature), while we continue to regard truly 'random' as a negative pole for outcomes inaccessible to science. We may then make the error of assuming that contingency lies somewhere between the two poles, combining explainability from the good end with unpredictability from the bad terminus. This situation may represent an improvement upon the error of fully conflating 'contingent' with 'random', but such a scheme remains quite wrong, and constitutes no real offer of acceptance for the narrative style. For this scheme merely awards second-class citizenship to a style tainted by the bad, but offering enough value for marginal acceptance into the realm of the elect.

We must, instead, insist that no such dichotomy exists, and that explanations cannot be graded on a single line connecting two poles, with higher status accorded to positions nearer the 'determined' end, and classical contingency in some middle status of marginal acceptability. Contingency represents a *different* style of explanation from classical scientific determinism, a style fully appropriate to narrative data, and offering just as firm and satisfying conclusions when properly applied to adequate information.

In terms of providing insight into the range and uses of contingency-based explanation in science, I found this book most valuable in its explorations and illustrations of the pervasive effect of scale differences upon the relative weights and appropriatenesses of contingent *vs* predictabilist explanations (and now, shame on me, for I am falling into my own trap of dichotomy!) – not really surprising since the editor intelligently fashioned this volume as an examination of the full range of scales from Chapter 1 on all of life in all of geological time to Chapter 7 on the culture of *Homo sapiens* over a few centuries. At least four important themes about scaling circulate throughout these papers:

I. The usual correlation of broad predictability *vs* contingency in details. In the most common situation, broad, global, general and long-term outcomes may feature predictable aspects, while defining details remain largely in the realm of contingency. Thus, for example, I am willing to grant that once mobile multicellular animal life evolves, bilateral symmetry for elongated body forms becomes a good prediction on grounds of biomechanical advantage. But the details of who and when – the fact that insects rather than the extinct opabiniids, or mammals rather than dinosaurs, dominate their appropriate environments today – remain in the domain of contingent explanation (see my book *Wonderful Life* for a full exposition of this argument). Similarly, for human history, I am confident that evolutionary theory would have been developed and accepted by nineteenth-century biology even if Darwin had never been born – but the fact that Darwin actually won the day, and by means of such a radical theory as natural selection, has made all the difference in details of history that powerfully affect the lives of millions.

For two (bad) reasons, this difference in scaling has led to a common discounting of contingency: (1) why fret about contingent 'details' if we can achieve prediction for important aspects of broad patterns; (2) contingent details don't affect general outcomes, so they 'wash out' in the long run. Both these common arguments are false. First, in our fractal world, big becomes an entirely relative concept, and surely not intrinsically superior to small or short. We ignore tiny and short-lived bacteria because we can't see them, but they rule the world of life, and always have (see my book *Full House*, entitled *Life's Grandeur* in the British version, for a full exposition of this argument). Who dares say that the little and the particular don't matter? Wouldn't the world be much better off if Beethoven had lived to write a 10th and 11th symphony, or Mozart had composed, in his mature 50s, tragic operas about *Hamlet* and *King Lear*? We will

never, never know such pieces, and we are thus all the poorer. But thank God that the sperm for J. S. Bach won the great impregnation lottery instead of the adjacent competitor that would have made a tin-eared brother or sister.

Second, contingent details do not necessarily wash out over time; rather, they make history forever after, body and soul. If Paul of Tarsus (not one of my favourite historical characters, by the way) had never lived, Christianity might well have sputtered and died aborning, remembered (if at all) as one of many short-lived and immediately forgotten Messianic sects.

Simmons makes this point particularly well in the concluding comment of his chapter: 'The lesson for archaeologists and historians ... who are minded to take an interest in the fluctuations of time, nature and humanity seems to be that change is unpredictable and contingent but has so far been towards the creation of dissipative structures producing ever higher amounts of entropy from the oxidation of fossil fuels to the loss of species.' Are not both claims equally important – the very general (and probably predictable) overall direction and the details that set the richness of history – for scientific history is the study and explanation of when and where.

Similarly, Bilsborough makes an interesting case for the origin of European Neanderthals from specific, chancy and unpredictable circumstances of a population bottleneck in Europe, allowing fixation of a set of features that had been less intensely developed in a more widely distributed population of ancestors. He then attributes the demise of Neanderthals (correlated with the invasion of their territory by modern *Homo sapiens*, that is by us) to contingencies of climate and geographic access. But this little bit of contingent history determined our current existence, so we cannot depreciate the importance of this particular local event, at least for our legitimately parochial concerns! He writes: 'If the origin of Neanderthals resides in contingent events, so too probably does their disappearance.'

I also greatly appreciate Bilsborough's apt metaphor of comparing these two levels of broad predictability and contingent detail with pitons and pathways: we may predict some sort of climb up the peak, but the path actually followed (one specific and explainable route among a very large set of potential and workable alternatives not taken) depends on the contingencies of where we hammered the pitons – and the route from piton to piton constitutes what we call history, and captures as much of the importance and fascination (also the science) of our past as does the general direction of the broad pathway. Bilsborough writes:

If speciation is prompted by isolating agencies that have little or nothing to do with adaptation *per se*, then contingency lies at the very core of the macro-evolutionary process. For the pitons will be hammered in, not at points necessarily corresponding to the shortest and most accessible route up to the peak, but randomly, according to the vagaries of isolation. And yet, as with mountaineering, the position of each piton determines the next phase of the climb.

2. What is predictable, and what contingent, often depends upon the scale under consideration, even for an identical event. For example (in the classic situation), a particular event (from which the actual direction of later history cascades) may be entirely determined and predictable in the immediacy of its local circumstances. (That is, if we knew the precise environments, and the crucial features of population dynamics, we could anticipate how natural selection would work on these fish in that pond to produce the key adaptation that made later invasion of the land, and the eventual evolution of terrestrial vertebrates, including our ultimate selves, quite predictable. But from the broader vantage point of millions of years down the evolutionary road, and given the vagaries of imperfect preservation for details of temporally distant singularities in the fossil record, this unique and locally predictable event becomes just one more contingency in the grand scheme of things.)

Conversely, we may lament, in the immediacy of the moment, that a particular event (an individual coin flip) has a random and utterly unpredictable outcome. But we may also fervently hope, as students of patterns over millions of years, for just this kind of randomness in individual events – since, ironically, such a situation gives us maximal predictability over long stretches of time. For extensive sequences of large numbers of similarly random events yield precise long-term predictability of general outcomes (close to 50:50 for thousands of coin tosses, but no clue to the particular outcome of a single toss), while precisely (but locally) determined initiating events yield unpredictability for resultant sequences – for we lose the evidence of such local determination when we gaze back through imperfect records many millions of years later.

Foley presents a striking example of this principle in arguing that natural selection may provide good predictability for a sequence of events once we know the starting point – but that particular starting points generally fall into the domain of contingency:

Response to novel circumstances, therefore, is strongly influenced by initial conditions which are stochastic, but the final outcomes are the result of strongly deterministic forces. ... Contingency helps us to set

out the initial conditions under which evolution occurs, natural selection provides us with rules governing responses in the evolving populations.

3. We often need, above all, to know the scale of an event in order to render a proper interpretation as contingent or predictable. Changing the scale often produces a surprising reversal of commonly assumed meaning for a superficially similar pattern. Paul's chapter rests upon this important theme. We generally assume that evolutionary trends result from natural selection leading to adaptation (a process usually construed as predictable). But most trends that we do note in the fossil record are actually too long and too slow to attribute to natural selection properly scaled up into geological immensity. Moreover, and most importantly, trends are surprisingly rare in the fossil record – too rare even to attribute to random walks, much less to a general bias for predictable selective improvement! Rather, at this largest of all scales in the history of life, stasis actively prevails – and we had better try to figure out why.

4. The very concepts of 'slow' and 'fast' – so critical in the basic attribution of predictability or contingency – are powerfully scale-dependent. At large scales, for example, events that might be leisureably observable over the course of a human lifetime may become instantaneous and invisible. Simmons, for example, makes the telling point that we have overemphasized the general predictability of a broad transition from gathering to agriculture because the domestication of a crop plant can occur in so short a time – as little as 20–30, but rarely more than 200 years – as to become invisible on time-scales of thousands of years in human history. Therefore, ironically, we selectively miss the large number of attempted transitions that failed, and also the surprising frequency of rapid reversion from cultivation to gathering. Consequently, by missing these details of fine-scale pattern, we may misconstrue the general process as more unidirectional. He writes: 'In the present context, the point is that such rapid transitions are likely to be archaeologically invisible and so many of the failed transitions or the deliberately reversed passages remain undetected.'

The theory of punctuated equilibrium is also based upon this same paradox – for events of branching speciation that are slow as could be on the scale of our lives (thousands of years in general) become instantaneous at general scales of geological resolution, where single bedding planes (that is, geological 'moments') usually compress several thousand years of history onto one unresolvable

layer. But traditional palaeontology made the crucial error of searching for continuity of change through strata representing millions of years – a time-scale that usually records the stasis of successfully established species, not the continual transitions of small, speciating populations. Paul writes:

Thus to detect trends induced by directed selection, we should be sampling through single beds or rhythms, not extensive sections tens or hundreds of metres thick. ... Once one has appreciated this time-scale it is easy to see why new species appear 'suddenly' in the fossil record. Even a species which evolved gradually over 10,000 years would appear within a single bed in the Cenomanian chalks of southern England.

The relation of the punctuationalist model to explanation by contingency

The authors of this book have particularly explored the strong relationship between the model of punctuated equilibrium (as first developed by Niles Eldredge and me in 1972, and most recently summarized in a coming-of-age article in *Nature* at the theory's 21st birthday in 1993) – and of punctuationalist models of change in general – and preferences for narrative accounts of history based on the predominance of contingency. Punctuated equilibrium is a particular, scale-dependent theory for the level of speciation in evolution. It argues, as a defining feature, that the bulk of evolutionary change does not occur by slow and continuous transformation of entire populations through long sequences of strata in geological time (a mode of evolution called anagenesis), but rather by the differential propensity of lineages to undergo events of branching speciation (a mode of evolution called cladogenesis) during periods of time (thousands of years in general) that may be slow by the scale of our lives, but are generally instantaneous on scales of geological resolution (where the 'moments' of single bedding planes usually span thousands of years). Once formed in a geological moment, species tend to remain stable throughout their geological duration – a substantial period that may average 5–10 million years for the mean duration of marine invertebrate species. Thus, evolution is not primarily a story of slow and 'purposive' change within lineages, but rather a tale of predominant stasis, punctuated every now and then by defining and geologically instantaneous events of speciation, with branching of descendant populations from stable (and usually persisting) ancestral lineages.

Although punctuated equilibrium strictly applies only to the

level of speciation, more general models of punctuational change may have broad application to other (or even to all) temporal scales in evolution and human culture – from the inordinate importance of such paroxysms as wars, conquests, and epidemics in human history, to the restructuring of entire biotas by mass extinctions induced by such instantaneous and global catastrophes as the impact of large extraterrestrial bodies (the now nearly-proven triggering cause of the last major mass extinction – the end Cretaceous event that wiped out dinosaurs along with about 50 per cent of all marine species, 65 million years ago).

In stating why the punctuationalist model provides so much scope and favour for contingency, while older preferences for gradualism implied general predictability, we should cite the two great subjects of macro-evolutionary study, as specified by G. G. Simpson in his definitive book of 1944, *Tempo and Mode in Evolution*. For tempo, gradualist models favoured slow and continuous transformation within single lineages over geological time. Most explanations for such grand and global continuity invoke predictable and lawlike causes like natural selection, moving lineages towards increasing biomechanical improvement. Punctuational models offer far more scope for contingency, for lineages now remain stable in their normal mode, and only change at unusual and unpredictable geological moments of branching. Change becomes an odd and rare event, not an intrinsic and predictable property occurring effectively all the time.

For mode, punctuational models favour contingency because sustained change now must 'step' through a series of speciation events, each initiated contingently by branching of a small population isolated in a restricted geographic area; based upon a complex and unpredictable regime of climatic and geographic change (to provide both the isolation required for branching, and the selective regime promoting subsequent change); and subject to the range of random processes (drift and founder effects) that are so potent in small populations but often weak to irrelevant in very large populations. By contrast, gradual change in global populations suggests a much greater scope for predictable and repeatable causes.

For example, the switch from gradual to punctuational perspectives has certainly granted greater scope to contingency in human evolution. The old view of a single human species at each period, propelled throughout our evolutionary history on a unidirectional trend to larger brains, suggested a predictive process regulated throughout by selection and adaptation. The current popularity of a revised family tree, replete with numerous contemporary branches at most times of our history, only one of

which eventually led to modern *Homo sapiens* – and with modern humans arising from one small population, branching in one discrete place from ancestral *Homo erectus* just a few hundred thousand years ago, rather than gradually arising over more than a million years by directional transformation of *Homo erectus* populations throughout the Old World – suggests a much chancier, much less guaranteed, much less repeatable evolutionary story replete with dominating contingency.

Foley's article stresses this theme by tracing human evolution through three episodes of multiple speciation events – the sequential radiations of early bipeds, megadonts (the robust australopithecines, not our direct ancestors), and the genus *Homo* (including our immediate ancestors from one line in a small bush of species). Bilsborough, whose own views have changed to allow more scope for punctuational models based on contingency, recognizes the linkage of conventional predictive schemes with the gradual and anagenetic views that he formerly favoured. On Wolpoff's theory of regional continuity for the origin of *Homo sapiens* from the worldwide *Homo erectus* populations of three continents (that is, the most strongly gradualist and predictive account), Bilsborough writes:

Despite the authors' protestations to the contrary, this is, in effect, the single species hypothesis in a refashioned form. It necessarily presupposes constancy of selection pressures on hominid populations, not only across the whole of the Old World, but also over the entire span of the Pleistocene. More particularly, it envisages a predominant and stabilizing influence for those pressures associated with socio-cultural acquisition and elaboration. The entire hominid evolutionary process over the last two million years is seen as progressive fine tuning to such a niche.

Three predominant themes linking contingency with the punctuational model recur throughout the papers of this volume:

1. The normal state of systems tends to active stability, not continuous change in a directional, predictable, progressive and adaptive direction. Authors defend such stasis across the broadest range of scales from the characteristic history of most species over millions of years in their geological duration (Paul), to the stability of English social organization (despite our received wisdom about continuity of technological change) from 1688 until the early to mid-nineteenth century (Bintliff).

Paul expresses the issue in a particularly succinct and telling manner:

Ever since Darwin palaeontologists have concentrated on documenting and explaining morphological change in fossils. What we should have been doing is trying to explain why fossils do not change. Stasis is a far more common phenomenon, and in an ever-changing environment, a far more puzzling one. Fortunately, stasis is now being taken seriously and more independent evidence of its abundance in the fossil record is emerging.

2. Change tends to occur in rapid events of perturbation leading to branching of lineages, not by directed transformation of entire systems. Again, authors apply this principle to a full range of scales, from Layton's demonstration of frequent shifting in human history between hunting-gathering and farming, over and over again, back and forth, in numerous and distinct populations (rather than a global and predictable movement to ever more complex modes of production); to Bintliff's documentation that the range of Roman villa size remained effectively constant throughout the period of Roman occupation in Britain.

3. Large-scale trends occur by a complex pattern of differential success of certain branches (species) within a bush of possibilities, not by slow and steady transformation of global systems. Bilsborough stresses how the shift from gradualist and anagenetic to punctuational and speciation models favours a greatly expanded role for contingency, and he frankly discusses his own change of opinion in this direction:

It is evident that the pattern of hominid phylogeny was appreciably more polyphyletic than many workers considered even half a decade ago, and certainly more speciose than I had appreciated it to be. ... Such multiple species greatly increase the probability that contingency has been a significant influence in human evolution. Punctuational theory together with studies of the genetics of small populations and of speciation mechanisms provide a conceptual framework for such findings and the likely processes involved ...

If the models preferred here at all approximate to the reality of human evolution, then contingency lies at its heart: contingency in the timing and intensity of the isolating or bottlenecking mechanisms; contingency in the size, composition and characteristics of the founding population that is isolated or preserved; contingency in the composition of the gene pool that is sealed off by the speciation process and, in the transience model, contingency in those parts of the genome that contribute the genetic environment for a particular gene complex with major developmental effects.

We students of the historical sciences must join with our colleagues from all scientific fields in the search for invariant properties that record the workings of timeless natural laws, and

thereby undergird the variety of overt events. But we should not favour this style of inquiry, and we should not regard such invariances as inherently more important results of our research. We must also cherish, and with just as much vigour and hope for general insight, the panoply of wondrous and unrepeatable particulars that grace and constitute any historical sequence of complex events – for particulars make history and set the most general of current circumstances with as much influence as any law of nature can wield. (We would not be having this discussion at all if a particular bolide had not, at a particular moment, struck the earth and triggered a series of particular events that wiped out dinosaurs and gave mammals a chance.) We must recognize contingent events as the motor of history – and as a source of explanation equal in power and accessibility to all the timeless and quantitative laws that science has always touted as a professional core. Cherish both the Cretaceous bolide and the inverse square law, the single founding species of the primate lineage and the general principle of natural selection. They all have made us, in equal but different measure.

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1 Selection and the fossil record

Chris Paul

Summary

Evolutionary trends in the fossil record occur over vastly too long a time period to result from selection. However, a null hypothesis that all morphological patterns in the fossil record are random walks can be rejected, not because evolutionary trends occur, but because they are far too rare. Under the null hypothesis apparent trends would be abundant. The overwhelming majority of fossil species exhibit stasis (i.e. no morphological change) over the vast majority of their stratigraphic ranges. Stasis probably results from a combination of random mortality in each generation, changes in the direction of selection between generations, which when time-averaged become indistinguishable from random selection, and the sheer complexity of the genome. Morphological changes (and new species) only arise when the mechanism maintaining stasis breaks down. This may happen when new ecospace becomes available or after a near-extinction event when the founder effect becomes significant. Ever since Darwin, palaeontologists have attempted to document and explain morphological changes in fossils. What we should have been doing is trying to explain why fossils do not change. Stasis has been ignored yet it is a far more common phenomenon.

Introduction

Whether or not we find structure in the fossil record depends to a large extent, I suspect, on what we expect to see. Steve Gould has

already outlined how, until he and Niles Eldredge proposed the idea of punctuated equilibria (Eldredge and Gould, 1972) the prevailing perception among evolutionary biologists was of gradual morphological change associated with anagenetic (unbranching) lineages. Now the idea that most morphological change takes place relatively rapidly at speciation events is the more widely accepted hypothesis (but see Sheldon, 1993 for a review of biases that may favour the punctuational model). However, it is not just biologists who have misinterpreted the fossil record. Palaeontologists, who are (or should be) familiar with it, often have similar misconceptions about the fossil record. Here I wish to present a cautionary tale about one such misconception.

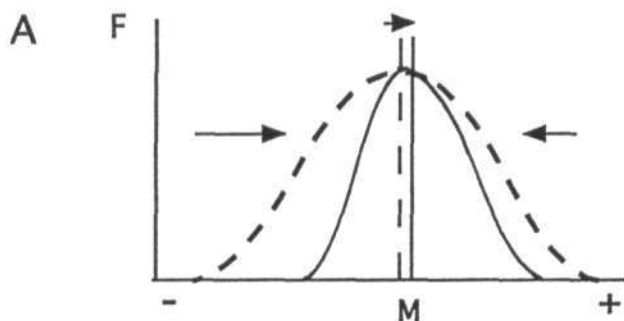
When Darwin wrote *On the Origin of Species* his task was, in effect, to convince the scientific world that species, which had previously been thought to be immutable, had in fact changed through time. Not surprisingly, he stressed how gradual the changes had been on a human time-scale. Since then gradual change has become entrenched in our minds, so much so that suggestions that other patterns might have occurred have sometimes been viewed as 'anti-Darwinian'. Darwin's mechanism for evolution was natural selection and so palaeontologists have sought what they regarded as evidence for the effects of selection (i.e. gradual change) in the fossil record. Given the vast numbers of fossil species, evidence for gradual change was inevitably found in what are now regarded as classic evolutionary lineages (e.g. *Micraster*, *Zaphrentis*, *Gryphaea*). These were hailed as proof of the reality of gradual change. No one (including myself) questioned that it took 40 years to find the first good example, nor that gradual evolutionary trends were, and still are, exceedingly rare. Darwin devoted two chapters of *On the Origin of Species* to explaining why the fossil record did not contain abundant evidence of gradual morphological change, and concluded that this could be explained by the imperfections of the record. This explanation has been accepted more or less ever since. To be sure, in Darwin's day the fossil record was very poorly known compared to present-day knowledge, but even now gradual evolutionary trends remain exceptionally rare. In many cases, to evaluate an hypothesis it is not enough just to find one or two examples which support it; we need to assess the balance of evidence for and against the hypothesis. Applying this approach to gradual evolutionary trends in the fossil record dramatically changes one's perception of evolutionary patterns. First, however, we need to consider how the effects of selection may be preserved in the morphology of fossils and what sorts of patterns might result.

Selection

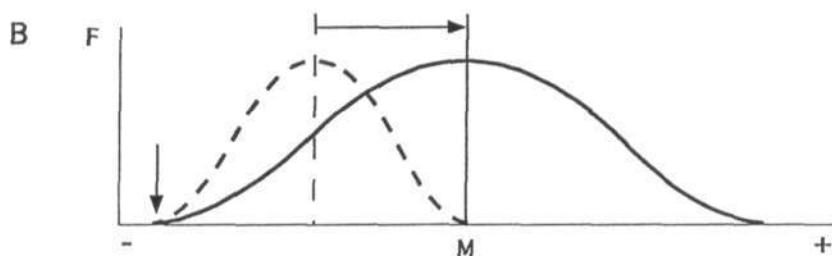
Selection may be thought of as acting in two principal ways: directed selection and stabilizing selection (Figure 1.1). Under directed selection (Figure 1.1a) selection pressures are more severe at one end of the distribution of a character than at the other and result in mean values moving towards the weaker selection pressure (smaller arrow in Figure 1.1a). Variance will remain effectively the same, or be slightly reduced, but under prolonged directed selection the population mean will gradually evolve towards the weaker selection pressure. The same result may be achieved by a relaxation of selection pressures at one end of a character distribution, in which case the mean will shift more and variance will increase (Figure 1.1b). Phyletic size increase is often the result of increased variance rather than increase in size of all taxa (Gould, 1988). Under the alternative, stabilizing selection (Figure 1.1c), selection pressures are equal at both ends of the distribution of a character and the population mean remains the same. Stabilizing selection was first demonstrated by Weldon (1901) in the shell of the European land snail *Cochlodina laminata* (Montagu) and has been reported in fossil oysters (Sambol and Finks, 1977). A third pattern, disruptive selection, in which selection pressures are most intense near the centre of a character distribution, is possible, but it is difficult to see how the normal distribution arose in the first place if the character was subject to disruptive selection. At best disruptive selection would seem to be a special case.

Morphological patterns

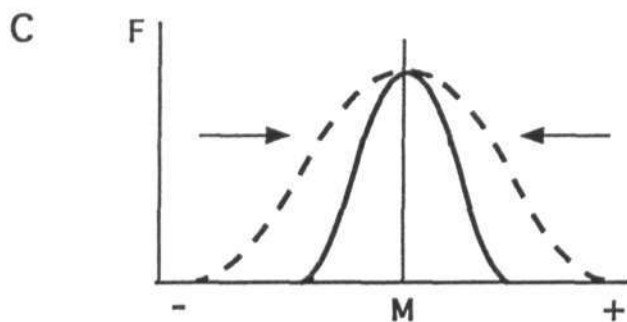
Patterns of morphological change, as observed in the fossil record, also fall into three categories: trends, stasis and random walks. Evolutionary trends (T, Figure 1.2) describe unidirectional change in a character, i.e. continued size increase, or continued addition of spines. Stasis (S, Figure 1.2) involves no significant morphological change, while random walks (R1 and R2, Figure 1.2) include reversals of change, e.g. size increase followed by size decrease; addition of spines followed by reduction in number. In theory, if selection is responsible for the patterns of morphological change seen in fossils, then evolutionary trends will result from continued directed selection, since directed selection drives the population mean in one direction. Stasis will result from continued stabilizing selection, since there will be no change in the mean of a character distribution, while random walks may arise if the direction of selection changes from time to time.



1.1a Directed selection



1.1b Directed selection: special case



1.1c Stabilizing selection

Key

F = frequency

M = population mean value

+ - Increase and decrease in a character (e.g. size)

- - - original distribution

— — — distribution after selection

- - - original mean value

- - - post-selection mean value

↔ direction and relative magnitude of changes

Figure 1.1 Effects of selection on a univariate character represented by a normal distribution curve

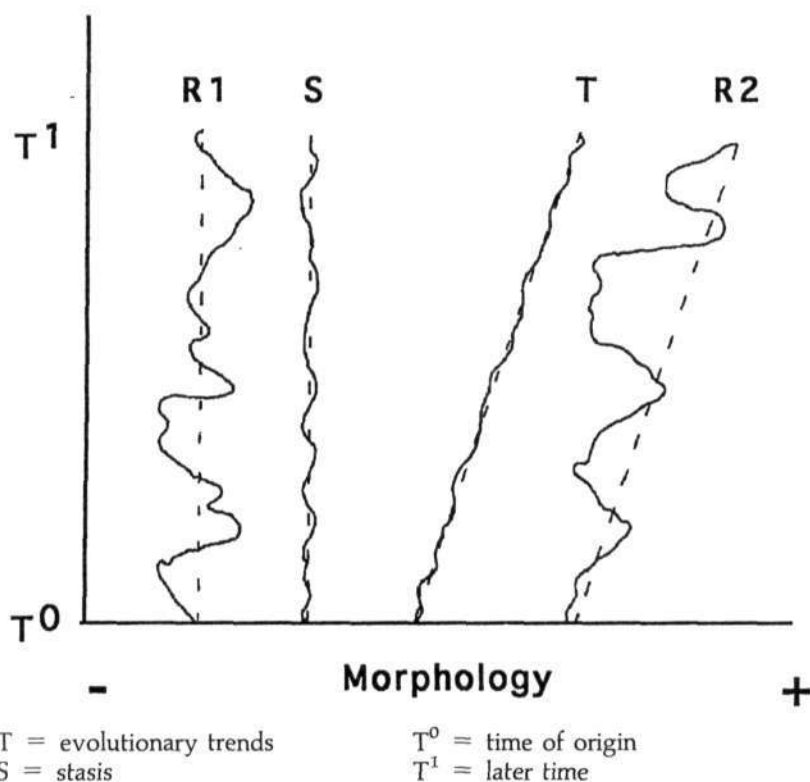


Figure 1.2 Patterns of morphological change

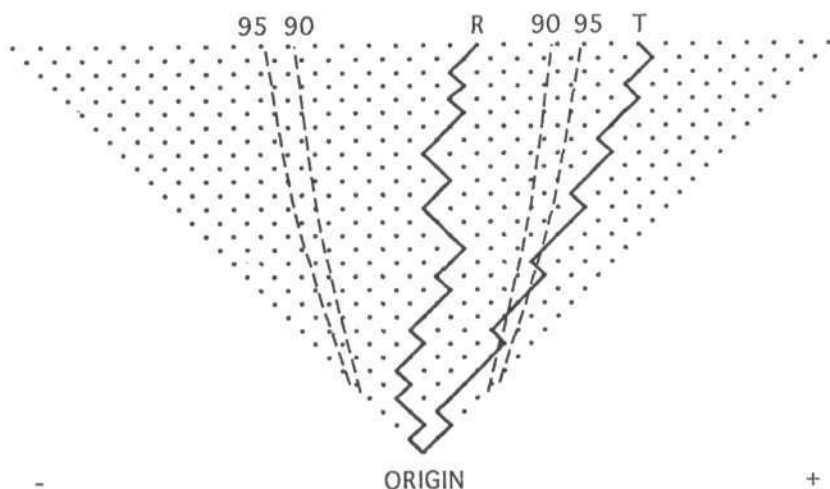
Difficulties

However, two related problems arise in considering data from the fossil record. Firstly, most evolutionary trends in the fossil record occurred over vastly too long a time period to have been caused by selection (Gould, 1990). For example, Lande (1976) estimated that one extra death per 100,000 individuals per year would account for all the morphological change in Gingerich's (1974) classic evolutionary trends in the Tertiary mammal *Hyopsodus*. Other mammal trends investigated by Lande lay in the range of one extra death per million individuals. Such weak selection pressures would be swamped by random mortality and even weak forces such as genetic drift (Lande, 1976; Gould, 1990). Morphological change in most classic fossil trends, e.g. *Micraaster* (Rowe, 1899), *Zaphrentis* (Carruthers, 1910), *Gryphaea* (Trueman, 1922), occurred far too slowly to be accounted for by directed selection.

The second problem concerns the scale of observation in the fossil record and is, in effect, the same problem stated the other way around. Much of my recent research has been concerned with the Cenomanian chalks of Western Europe. Sections are typically rhythmic with fairly regular alternations of purer chalk and more clay-rich marl a few decimetres thick (e.g. see sections in Gale, 1989). The rhythms are almost certainly orbitally forced with each pair of beds representing the precession cycle (Gale, 1990; Lamolda et al., 1994), which lasted about 20,000 years in the Cretaceous (Berger and Loutre, 1989). On average then, each bed represents about 10,000 years, which is adequate time for significant morphological change under directed selection. Thus to detect trends induced by directed selection, we should be sampling through single beds or rhythms, not extensive sections tens or hundreds of metres thick. Even if this were attempted in the Cenomanian, burrowing organisms have seriously mixed sediments within beds and it is extremely unlikely that any clear trend would be apparent. To detect patterns of morphological change induced by selection in the fossil record, varved sections, which record deposition annually, should be used (Paul, 1992). Once one has appreciated this time-scale it is easy to see why new species appear 'suddenly' in the fossil record. Even a species which evolved gradually over 10,000 years would appear within a single bed in the Cenomanian chalks of southern England.

Null hypothesis

So if the time-scale is completely wrong, do reported evolutionary trends in fossils represent random patterns that just happen to involve more or less unidirectional change? This idea can be investigated by erecting a null hypothesis that all morphological patterns in the fossil record are random walks. The null hypothesis predicts that 5 per cent of all morphological variation will lie outside the 95 per cent confidence envelope for random walks (Figure 1.3) and present sustained unidirectional morphological change, i.e. apparent evolutionary trends. The null hypothesis can be rejected because trends in fossils are far too rare! Even if every single example of a lineage that has ever been claimed to show a trend is uncritically accepted as valid, trends in fossil lineages are vanishingly rare. Furthermore, almost all research on evolution in the fossil record has concentrated on those taxa that show morphological change and/or those parts of their stratigraphic ranges where the changes occur. For example, *Micraster* ranges from the Lower Cenomanian to the Upper Campanian at least (about 25 million years), yet Rowe's classic evolutionary trends (Rowe, 1899)



R = random walk

T = evolutionary trends

Dots represent all possible positions for a 30-step random walk

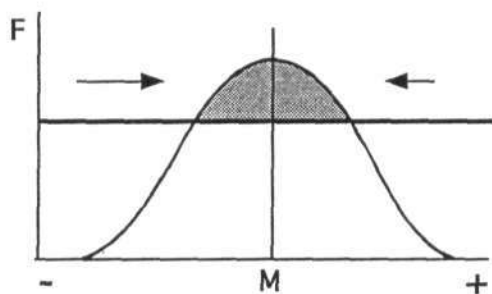
Figure 1.3 Null hypothesis prediction of morphological variation

occur only in the Turonian to Lower Santonian (about 8 million years). No-one reports examples of stasis; after all evolution involves change. Thus, despite the extremely biased documentation of trends in the fossil record, they remain stubbornly rare. They have certainly not been overlooked. Under the null hypothesis trends would be abundant. If the average fossil had 20 morphological characters, the number of trends should equal the number of fossil species. The inescapable conclusion is that, far from directed selection (or any other effect) driving morphological change outside the 95 per cent confidence envelope for random walks and thus creating genuine evolutionary trends, something has very effectively prevented this happening. Stasis was overwhelmingly the normal state of affairs, especially given the time-scale problems outlined above. This conclusion ought not to be so surprising. If stasis did not dominate the fossil record, palaeontologists would find it extremely difficult to recognize fossil species. If the null hypothesis were true, every character would be in a continuous state of flux and no two fossil populations would preserve the same combination of character states. It would be impossible to detect limits to this variation. As it is, fossils indistinguishable from living species (the genetic composition of which is understood) can be detected well back into the Late Tertiary and even earlier (e.g. Rayner and Waters, 1990).

Consequences

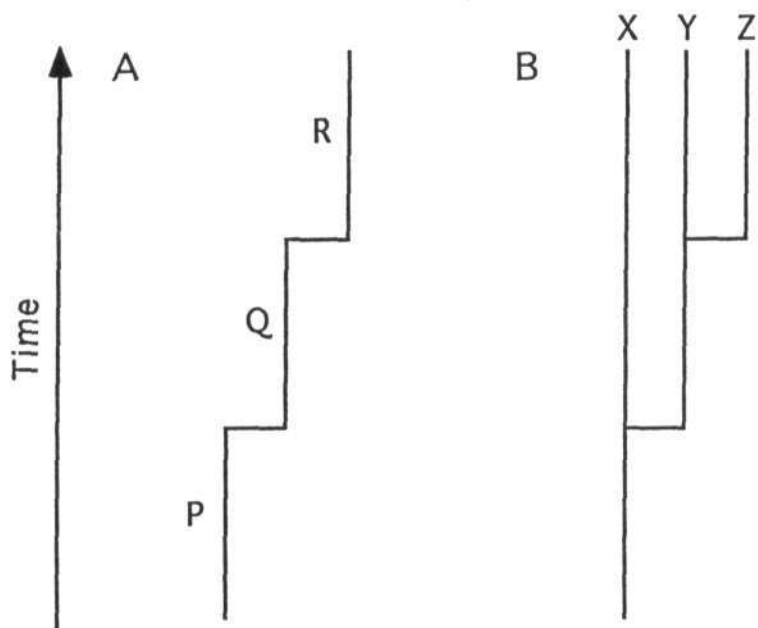
If stasis was so dominant, it must have been caused by some very simple and pervasive mechanism. I suggest that it results from three things: random juvenile mortality, changes in the direction of selection, and the presence of unlinked characters. Random mortality includes anything which unselectively prevents genes being passed on, such as unfertilized gametes, or the feeding of baleen whales, in the course of which millions of tiny plankton are consumed at each swallow. Mayr (1970) was right to argue that selection still affects those plankton that remain uneaten, but the range of morphs/genes available to selection is inevitably reduced. Where random mortality removes most individuals, only common morphs will normally breed. Unstable environments cause changes in the direction of selection. Fisher's classic study (1930) may have demonstrated that even small selective advantage will ensure the spread of a gene through a population, but this will only happen if the gene remains advantageous through many generations, i.e. if the direction of selection remains constant. Indeed the mathematical modelling that underlines Fisher's (1930) and Lande's (1976) papers is totally unrealistic in assuming not only a constant direction of selection, but a constant rate of selective pressure too. Sheldon (1996) has pointed out that this probably accounts for the discrepancy between rates of evolution observed on short and long time-scales. Unstable environments continually change what is selectively advantageous. Time-averaged through many generations, as most data from the fossil record are, the effects of directed selection in an unstable environment may be indistinguishable from those of random mortality in a single generation. Random mortality is effectively the survival of the peak of the distribution curve (Figure 1.4). If the arrows in Figure 1.1 are superimposed on the tip of the distribution curve in Figure 1.4, the relative strengths of random mortality versus directed selection can be seen. Clearly very strong and very persistent directed selection is required to counteract the effects of random mortality. Persistent directed selection may well require a stable environment (Sheldon, 1990, 1993). Finally, the size and complexity of the genome may promote stasis, especially where numerous unlinked characters are concerned. Extreme selection against one character may be totally random with respect to another unlinked character, even if the result of a severe population crash.

If stasis is the norm, rapid morphological change (including the evolution of new species) must occur under exceptional circumstances when the stabilizing mechanism breaks down. This will still



F = frequency
M = population mean value

Figure 1.4 Random mortality: survival peak of the distribution curve



A = anagenesis
B = cladogenesis

Figure 1.5 Gradual and abrupt morphological change

be a common phenomenon given the millions of parent species that existed over geological time. There has been a tendency to equate gradual evolutionary change (i.e. trends) with anagenesis (Figure 1.5), where no true speciation occurs, and abrupt morphological change (punctuated equilibria) with cladogenesis (Gould and Eldredge, 1993). I do not see the link, especially given the

dominance of stasis in the fossil record. Anagenetic changes, such as those in the chalk sea urchin genus *Hagenowia* (Gale and Smith, 1982), appear to me like cladogenesis in which the parent species failed to survive and they are strongly punctuational. Again, however, anagenetic lineages are so common that if they involved protracted unidirectional morphological change, true evolutionary trends would be abundant in the fossil record and they are not.

If stasis results from random mortality then the idea that new species arise when the stabilizing mechanism breaks down, implies that mortality was extremely low. Only when individuals with a wider range of characters survive to reproductive age will new variants breed and become established. The opening of new ecospace is one possible scenario; recovery after a near-extinction event is another. The progeny of those individuals which did survive will have very few competitors and the founder effect may become highly significant. The success of selective breeding by humans in producing wide morphological variation (if not new species) occurs not only because of our control over which individuals breed, but also because we ensure that as many progeny as possible survive up to the point of selection, thus making the widest range of morphs available from which to select.

The hypotheses that stasis results from a combination of random mortality, randomized selection, and the inertia of the genome, and that new species only arise when the stabilizing mechanism is relaxed, are testable. They predict that species with low fecundity but high investment in each offspring will speciate more frequently than those with high fecundity but low investment. For example, it would explain the higher speciation rates and shorter time-spans of mammal species versus bivalve species (Stanley, 1977). Equally, if the time-averaged effect of changing environments is to randomize the direction of selection, this would explain Sheldon's (1990, 1993) counterintuitive observation that stasis is associated with unstable, and trends with stable, environments; his 'plus ça change' model (Sheldon, 1996).

Conclusions

Most recorded patterns of morphological change in the fossil record apparently occur over vastly too long a time period to result from the effects of selection pressures. However, a null hypothesis that all morphological patterns in the fossil record are random walks can be rejected, not because examples of evolutionary trends occur, but because they are far too rare. Under the null hypothesis apparent trends would be abundant. The overwhelming majority of fossil

species exhibit stasis (i.e. no morphological change) over the vast majority of their stratigraphic ranges. I suggest that stasis results from a combination of random mortality in each generation, changes in the direction of selection from generation to generation which when time-averaged become indistinguishable from random selection, and the sheer size and complexity of the genome. It follows that morphological changes (and new species) only arise when the mechanism maintaining stasis (whatever it is) breaks down. This may happen when new ecospace becomes available or after near-extinction when the founder effect becomes significant. Ever since Darwin, palaeontologists have concentrated on documenting and explaining morphological changes in fossils. What we should have been doing is trying to explain why fossils do not change. Stasis is a far more common phenomenon, and in an ever-changing environment, a far more puzzling one. Fortunately, stasis is now being taken seriously and more independent evidence of its abundance in the fossil record is emerging (see, for example, Brett and Baird, 1995; Coope, 1994; Lieberman et al., 1995; Morris et al., 1995).

Postscript

When I began research I used to think that the most seductive (and therefore potentially misleading) ideas were those one wanted to believe. Now I suspect there is an even more pernicious group: those that are so eminently reasonable that no-one questions the assumptions on which they are based. Directed selection causes gradual change; classic fossil lineages exhibit the expected change; *ergo* the fossil record preserves evidence of directed selection. In practice the time-scale is all wrong and by far the vast majority of fossils do not change at all. Stasis rules, OK?

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2 Evolution and environmental controls: Palaeozoic Black Deaths

Michael House

Summary

The role of error and speculation as stimulants to scientific advance is intriguing. Often the solid pursuit of the scholar, however renowned, does not achieve innovation. Rather a wild idea, especially a wrong one, will concentrate international research on a problem, and this will often lead to a major advance in knowledge. This paradox is illustrated by several examples. The many periods of extinction known in the fossil record of the Phanerozoic (from 570 My (= million years)) led to the suggestion that these indicated a 26 My periodicity; this theory still spawns a flood of interpretations from astronomers. But the factual basis for the hypothesis seems flawed. This is illustrated by the 340 My history of the ammonite group. The idea that evolution is, at a low level, punctuated by crisis rather than gradual change was claimed to be anti-Darwinian and an intellectual breakthrough (although who better than Darwin would have known storm from calm); resulting studies have shown the living world is more subtle than speculators on it. But significant periods of crisis are known, and are increasingly being precisely documented. Some seem to represent periods of intensely warm climatic excess, and are indicated by widespread hypoxic and black shale events internationally, suggesting hostile environments which may have led to extinctions.

But do these represent climatic maxima, and are these regular, and controlled by orbital factors? At another level, is periodicity a major factor after all?

At a conference in Durham, in a Norman city, with a Norman castle and cathedral, it is appropriate to remember that the Bayeux Tapestry illustrates the arrival of Halley's Comet, coinciding with the Norman Conquest, in 1066. The comet is also recorded in the *Anglo-Saxon Chronicle* for that year. Halley's Comet has returned every 76 or so years since. Unusual changes in the heavens have probably always had this wonderful aspect of reminding tremulous human souls about potential doom. The most recent comet return has been associated with discussions about periodic extinction through geological time. It has also come at a time when sedimentary cyclicity in sedimentation during the last 570 million years (which comprises the Phanerozoic) has been increasingly studied (Figure 2.1).

My concern in this chapter will be about environmental changes leading to extinction in the past. I want to take a quite different approach from that demonstrated in the contributions of Steve Gould and Chris Paul and rather than review how thoughts and conceptions on the evolutionary process have changed, say a little about the problems that palaeontologists and those interested in evolution have with the facts. My emphasis will be on the rigid constraints that the changing environment imposes on how evolutionary change can be exploited and to consider the contingency parameters of the environment as an evolutionary control. This is deliberately to exclude consideration of genetics, adaptation, ecology and other familiar aspects of evolutionary theory, which have been exhaustively covered many times, and the importance of which I do not wish to minimize in any way. I will also advance the idea that in science wrong ideas can often act as an incredible stimulant, leading to major advances in knowledge. Perhaps in some cases they are the greatest stimulant to advance.

Sedimentary periodicity in geological time

In 1977 a seminal paper by Vail, Mitchum and Thompson argued that the evidence of sea-level changes through geological time suggested the operation of cycles at differing scales. These were related to periods of rise and fall of sea level which had effects of moving shoreline position, and altering the sedimentary environment from time to time. Long-term cycles, termed those of first order, represented periods of perhaps around 300 million years (My); those of the second order suggested periods of 10–80 My;

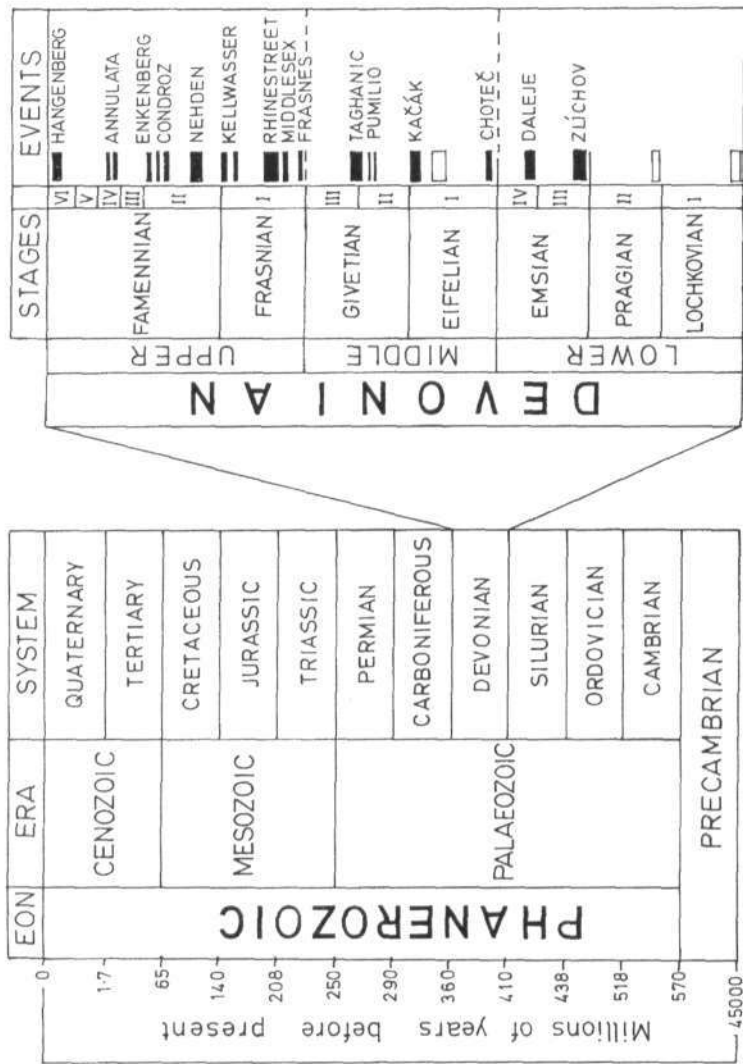


Figure 2.1 The geological time-scale and sequence of stratigraphical systems

those of the third order were cycles with periods of between 1–10 My. No evidence was given to suggest that the cycles had any exact length. Lesser cycles are thought to be related to changes in the orbital pattern of the Solar System. Such analyses have led to a recognition of worldwide changes of sea level and hence, that an important control of the environment for life on earth is in near-constant flux. These basic ideas are old but their new application in seismic and sequence stratigraphy, combined with high resolution biostratigraphy, has introduced quite new tools for examining evolution in time.

Such changes would be referred to by several American authors as stochastic, or contingent, in relation to their effect on evolution, but one must recall the wise and shrewd comment of Charles Darwin on factors which 'we, in our ignorance, think to be due to chance'. Part of the fascination of detailed international correlation work by biostratigraphers is the evidence they provide towards the understanding of such events.

Claims of periodicity in evolution

It would be true to say that in the last decade or two, palaeontologists have lived in interesting times. How far this was related to the return of Halley's Comet in 1985 and 1986 it is difficult to assess, but a few years before and the decade after witnessed a spectacular burst of interest and speculation about extinction. There has been much topical interest in the problem of the extinction of the dinosaurs at the end of the Cretaceous (the K/T and Mesozoic/Tertiary boundary). The publication in 1980 of the discovery by the Alvarez team of an iridium anomaly actually at the boundary was followed by their suggestion that, since such concentrations are only known from cosmic material, then cosmic dust clouds could have caused the extinctions. Gloomy scenarios of asphyxiation and global darkness, Strangelove oceans and cometary impacts were postulated to explain extinctions, not only of dinosaurs, but of ammonites and belemnites, rudist bivalves and other fossil groups at the end of the Cretaceous.

This was all very popular stuff, and instantly entranced science magazine readers and Sunday paper devotees. At about the same time, and doubtless conceptually related to the comet's return, we had the stimulating papers by Raup and Sepkoski (1982, 1984) claiming that when they analysed diversity through time, and by that they meant totting up the number of families at intervals through geological time, it appeared to give evidence of periodic extinction of about 26 million years. Well, of course, linked with the

ideas of the arrival of comets, this led astronomers to produce a plethora of interpretations on how such effects might have been produced. Oscillations, at various frequencies, in the movement of the Solar System in its orbit around the Milky Way galaxy, taking it in and out of zones with hazardous galactic material, was one hypothesis. Another invoked a Companion star, which might periodically sweep into the Oort Cloud to produce cosmic showers; yet another proposed a nemesis star which will eventually destroy us completely. These were not the only hypotheses. It is appropriate to say that the only voice speaking against this speculation by astronomers has been the Durham resident, the then Astronomer Royal, Arnold Wolfendale, who, having analysed the documentation on the position of the Solar System over the past 200 million years, took the view that it has never been placed where such scenarios are appropriate. But theories are still growing on the assumption that the basic periodicity in extinction is correct. It is the correctness of that hypothesis of periodic extinction which I wish first to pursue.

Ammonoid evolution

The ammonites and goniatites, or Ammonoidea, are coiled shells of ancient cephalopod molluscs which lived in marine waters. They are first found as fossils in rocks of the early Devonian (about 390 million years ago) and almost certainly became extinct at the Cretaceous/Tertiary boundary (about 65 million years ago). Although it has been claimed that early Tertiary examples have been recorded in Turkmenia and Antarctica, neither claim is convincingly authenticated. The group thus existed for about 325 million years (Figure 2.2). Because the ammonoids evolved very rapidly they can tell time to the geologist as well as coins do to the archaeologist. The span of their existence is divided into hundreds of zones in which we can document the genera and species occurring at any particular time. The zones are time-diagnostic by the occurrence in them of forms not known elsewhere. Thus the Ammonoidea form the most precise time-scale for correlating marine rocks internationally through the time of their existence. The forms are grouped into families, and higher divisions, which form useful categories for the analysis of diversity of the group through time and the periods of high extinction and diversification.

The work of many specialists on the ranges of genera and families of the Ammonoidea was collated some years ago (House, 1989), so that a new analysis could be made of extinctions through the 325 million years of the history of the Ammonoidea. It was

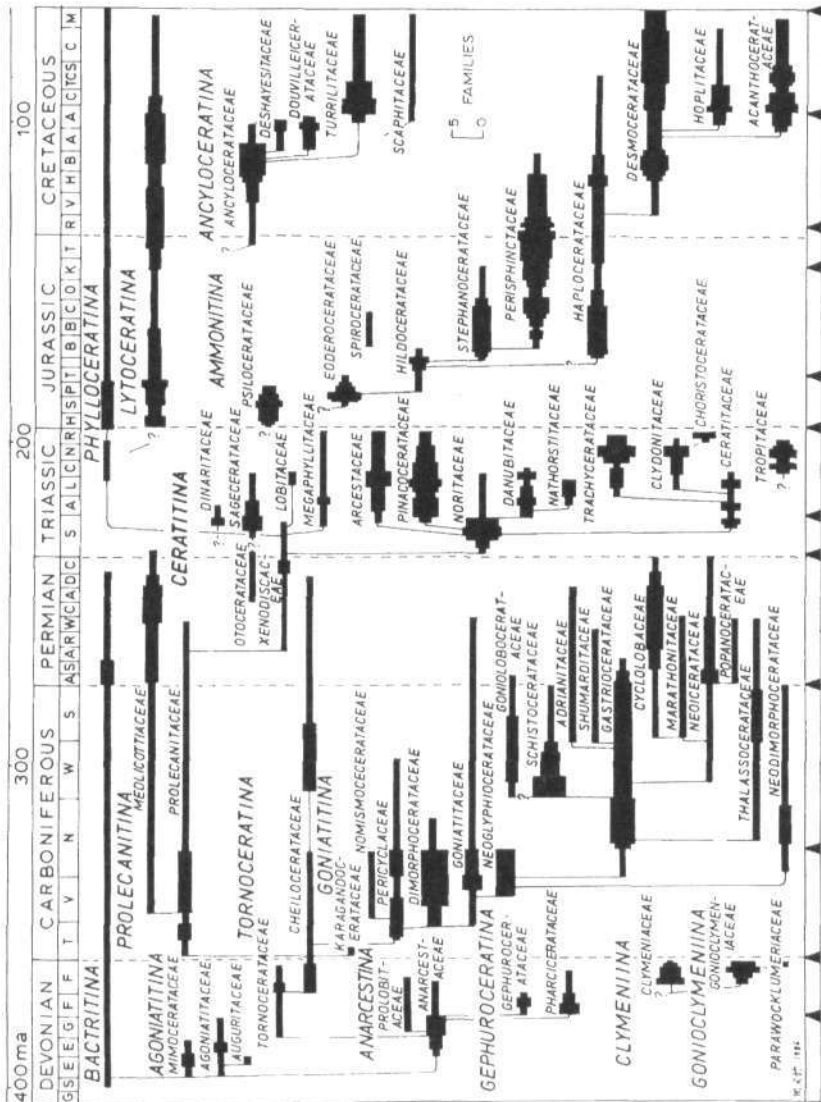


Figure 2.2 Ammonoid evolutionary tree: Devonian to Cretaceous

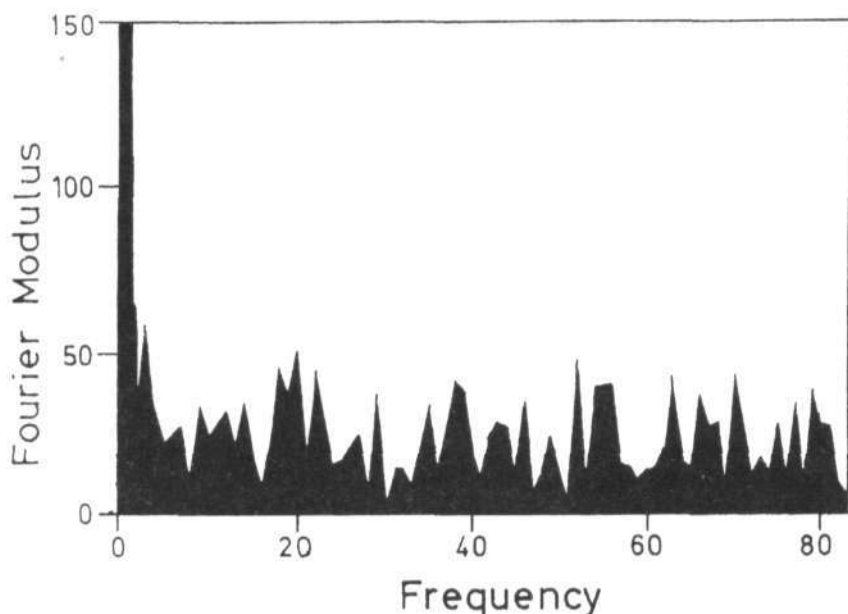


Figure 2.3 Fourier analysis of periodic extinction. Frequency scale in million years, Fourier modulus indicates extinction frequency

possible to assess numbers every two million years through this period, so that there were about 160 time data-points, whilst the intervals were all equal, as nearly as could be ascertained by current estimates of radiometric dating through the period. This represented over three times the data set size available to Raup and Sepkoski and offered a significant refinement. Furthermore, Raup and Sepkoski were obliged to work on the assumption of equal time intervals for the geological stage intervals, although that is an unlikely situation, whereas the new compilation was estimated at an even two-million-year interval.

No evidence for periodic extinction was forthcoming after Fourier analysis of the data (Figure 2.3). That is, whilst there were many extinction events, it could not be demonstrated that the periods between any were regular or that there was a peak at 26 My. On the other hand, new evidence of marine transgression and onlap onto continental shelves suggested a correlation between diversity and the extent of shelf seas. This exemplifies how the work of Raup and Sepkoski, although now not acceptable to most, did concentrate attention on extinction events in a way that has led to detailed and rewarding contributions to knowledge by others.

The fluctuations in the evolution of the Ammonoidea are considerable, and the main extinction periods, the end-Devonian, end-Permian (end-Palaeozoic), end-Trias and end-Cretaceous events are especially well marked (Figure 2.2). These reflect the manner in which the ammonoids were affected in the same way as other groups at these times. The major extinction periods were recognized early in the last century and enabled geologists to establish major geological boundaries at some of these points. Of course, diversity of taxa (numbers of families or genera) is not the same thing as contemporary abundance, and the generic and family divisions are arbitrary divisions of different systematists, and can only be regarded as comparable with the greatest scepticism. Nevertheless this type of data represents, as Raup and Sepkoski accepted, about our only way for numerical analysis of evolution in time.

Devonian Anoxia, black shales and extinction events

I now wish to turn to something which is very much a current problem, and an exceedingly interesting one, relating to the Devonian period, some 360–417 My ago (although these estimates based on radiometric dates are not very precise). One of the features of this time-span is that it included a series of events which are recognizable in sedimentological terms all over the world. About ten of these have been given specific names, related to sedimentological perturbations, traced in many areas of the world, which seem to represent specific and strange interruptions (Figure 2.1). Often these are characterized by black shales, or black limestones, as seen in marine rocks. Some particularly well known ones are named the Daleje Event (late Lower Devonian), Choteč Event (lower Middle Devonian), Kačák Event (mid Middle Devonian), Rhinestreet Event (early Devonian), Kellwasser Events (late early Devonian), Annulata Event (mid late Devonian) and Hangenberg Event (Devonian/Carboniferous boundary). Associated with these, and the other events, are evolutionary perturbations, and these have been especially well documented in relation to the evolution of the ammonoids (House, 1985).

What is the interpretation of these black shale and black limestone events? Normally the sea floor is oxic and occupied by a diverse biota, including benthos and endobenthos, which may live in burrows, temporarily rest within the sediment, or actively live on organic material within the sediment. The result is that sediments are churned over many times and bioturbated. Many of the black sediments of the above events do not show this but indicate by their precise primary lamination that no benthos or endobenthos

disturbed the sea floor sediment. It is interpreted that at these times either anoxic (no oxygen) or hypoxic (low oxygen) conditions prevailed. Also total organic carbon (TOC) levels are high at these times, indicating that primary organic debris was not being eaten and recycled by the biota of the sea floor: It is at these times, too, that hydrocarbons may be preserved. Thus anoxic events provide petroleum-source rocks. Sea-level rise bringing low-oxygen waters over the shelves may be one possible explanation for these events. But was this rise triggered by tectonic events or climatic events? The identity of the primary causes is still uncertain.

In 1970 Digby McLaren drew attention, not so much to the sedimentological changes at the Kellwasser Events, but to the evolutionary extinctions associated with them. He invoked meteorites or bolides hitting the earth to explain these sudden extinctions (see also McClaren and Goodfellow, 1990). This was taken up, as already mentioned, by the Alvarez team in 1980 to explain iridium anomalies at the Cretaceous/Tertiary boundary and the extinction of the dinosaurs and ammonites, which in turn led to the development of the hypothesis that the earth had periodically entered areas of space where it suffered bombardment by meteorites, bolides and cosmic dust clouds. As we have seen, in the light of new analyses of the data, this now appears untenable. That is, evidence for the actual arrival of meteorites is clear enough and is being increasingly well documented, but there seems to be no evidence of regularity.

The extinction sequence at the Kellwasser Events (Figure 2.4) has now been analysed in very great detail, not only for ammonoids (Becker and House, 1994), but for other groups also (Klapper et al., 1994). It is clear that the extinction event has a pre-history and post-history. Many species and genera of ammonoids became extinct at the Lower Kellwasser Event, many more at the Upper Kellwasser Event. But if one takes only the hypoxic level of the Upper Kellwasser limestone, trilobites appear to have become extinct with the start of the hypoxic facies, whilst ammonoids are abundant in the actual hypoxic facies, only to become extinct as it ended, perhaps with a global regression of the sea; conodonts follow a similar pattern. There then followed an evolutionary lull, characterized by one particular opportunistic ammonoid named *Phoenexites frechi*, and later there was a new radiation of ammonoids giving a novel burst of evolution – presumably exploiting environments left vacant by those which had become extinct. This extinction history is expressed in a series of sedimentological signatures, and the association of the extinction with a Black Death, associated with the black anoxic limestones or shales, is only part of

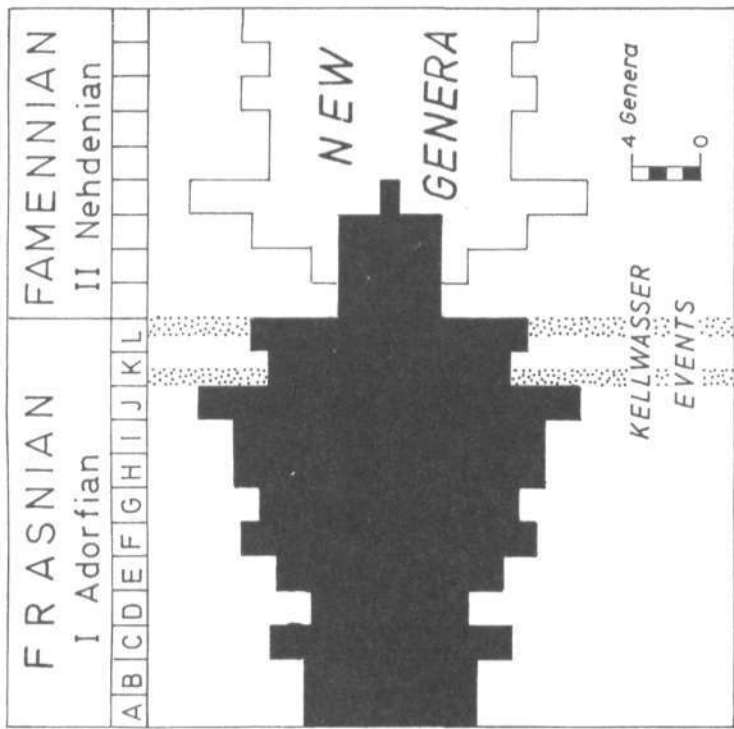
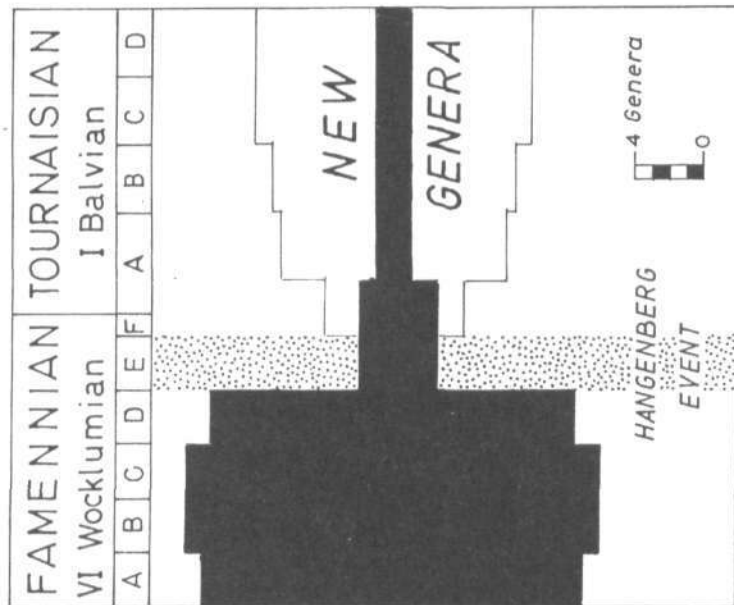


Figure 2.4 Ammonoid extinction: Kellwasser and Hangenberg Events

the story: the pattern does not seem the sudden sharp event one would expect of a bolide, and this was clear many years ago (House, 1985).

Although it has not caused as much excitement in the popular literature, the extinctions at the Hangenberg Event (Figure 2.4b), at the Devonian/Carboniferous boundary, are rather similar. An appropriate black shale interval is seen in the Rocky Mountains (the Exshaw Shale), in Germany (the Hangenberg Shale), and in a black shale level in southern France, Morocco, and even in China. Again there is an association of sedimentary perturbation with an evolutionary break (House, 1985; Becker, 1993).

Other events, earlier in the Devonian, those named the Daleje, Choteč and Kačák Events, are also associated with sediments which appear to have formed in hypoxic conditions; these are best documented in the European area and North Africa, and are characterized by abundant pelagic dacroconarids, forms analogous to modern pteropods which form ocean oozes at the present day, suggesting sea-water deepening. Also curious large bottom-dwelling bivalves, such as *Panenka*, indicate odd sea-floor conditions.

Other late Devonian events are also associated with black shales and are widespread. The Rhinestreet Shale of New York seems to represent a maximum deepening associated with hypoxia and this aligns approximately with the bituminous Domanic facies of northern Russia and even a significant transgression in Australia: a global event is inferred, but a considerable amount of time is involved in the Rhinestreet Event. Higher in the Devonian the Annulata Schiefer of Germany similarly aligns with the Three Forks Shale deepening in the mid-West of the USA and with similar facies in North Africa and Western Australia.

So not only has it proved possible to document environmental changes as indicated by the sedimentary perturbations internationally, but the exciting thing is the way in which they appear to be related to extinction events, or unusual and widespread abundances of particular organisms. Now the interpretation of these events has proved to be very interesting and I think, first of all, it makes a bolide interpretation difficult to sustain, largely because of the successional history associated with each event, and the time involved: they are not instantaneous events. Rather there is an environmental perturbation, resulting in widespread anoxia at some stage. The cause may be ocean overturn, perhaps with transgression of the seas, possibly due to plate tectonics, carrying environments inhospitable to many groups over the shelf sea areas of the globe, and leading to either extinction, or temporary abundance of unusual taxa. Another hypothesis suggests the proximal cause may be

climatic, and, amongst many hypotheses, sharp, sudden temperature rises and greenhouse effects have been invoked.

Rhythmic environmental change

Stephen Jay Gould has long been associated with advocacy of a model for evolution – punctuated equilibrium – where very long periods of minimal evolutionary development are interrupted by geologically short phases of rapid evolution. I want now to say something, not about punctuated equilibria – but how impossible it is for us to think that we can test them in the fossil record. It is not just that what we see in the fossil record is the phenotypic expression of the genetic character, which is the only meaningful element for the study of successional evolution; but that inherent in geological history has been a series of fluctuations in the geological record which every experienced geologist sees whenever he goes to any pelagic (deep sea) sequence. That is to say, the sedimentation is to a greater or lesser extent rhythmic. Occasionally there may be episodes of considerable change and at other times less obvious evidence. But one thing is certain: it is clear there is continuing evidence of changes in the environment.

Now the really intriguing question, which many of us are involved with now, is whether some of these rhythmic patterns may reflect climatic changes – with associated modifications in temperature, rainfall, weathering of rocks on adjacent land, and transformations in the nature of resultant sediments in nearby sedimentary basins. And whether these changes may be driven by orbital oscillations and hence they may be of some use for establishing time-scales. Regular small-scale rhythmicity, termed couplets, are often arranged as groups of about five couplets forming a bundle. The possibility exists that this pattern represents the interference of the Precessional orbital oscillations (about 23,000 years) with those of Eccentricity (about 410,000 years) (Figure 2.5). This interpretation for many sequences is seen increasingly to be the only rational explanation of constant interference ratios of this sort. If true, it opens up the possibility of a new type of time-scale for the past with a far greater resolution than anything we have at the present.

The effect of orbital changes on the insolation, or solar energy, reaching the outer parts of the earth's atmosphere is considerable. The variation can be up to 5 per cent of the total average energy, or up to 100 watts per square metre. Climate will be affected through complex alterations in weather systems. The major such oscillations are the Precession, Obliquity, and Eccentricity Cycles (Figure 2.6).

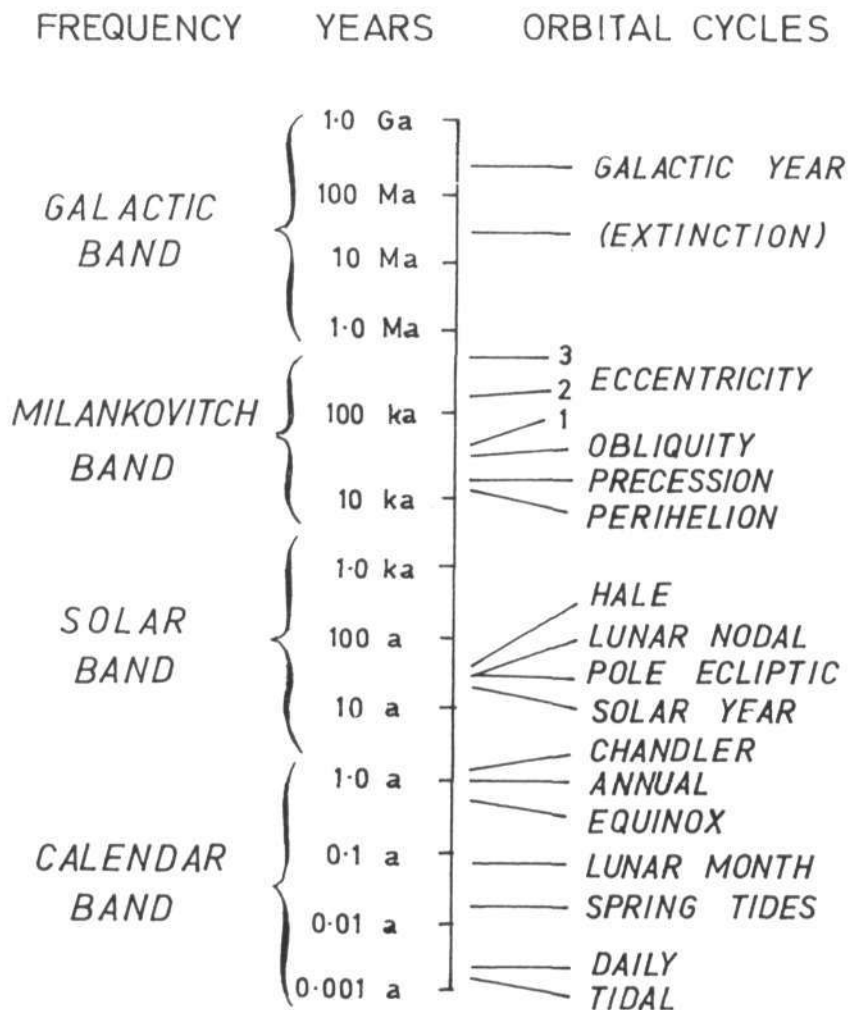


Figure 2.5 Rhythmic environmental change

The Precessional Cycle (or pseudocycle) combines oscillations at 19,000 and 23,000 years. Recognized first by Hipparchus in 129 BC, it reflects the fact that the axis of the earth's rotation (the projection of which today in the northern hemisphere lies near the Pole Star, Polaris), precesses through an ellipse through time, changing the timing and nature of the equinoxes. The Obliquity Cycle (about 41,000 years) is caused by the fluctuation in the angle the earth's rotational axis makes with the plane of the orbit and this varies by about 3.5 degrees, sufficient to take certain areas in and out of

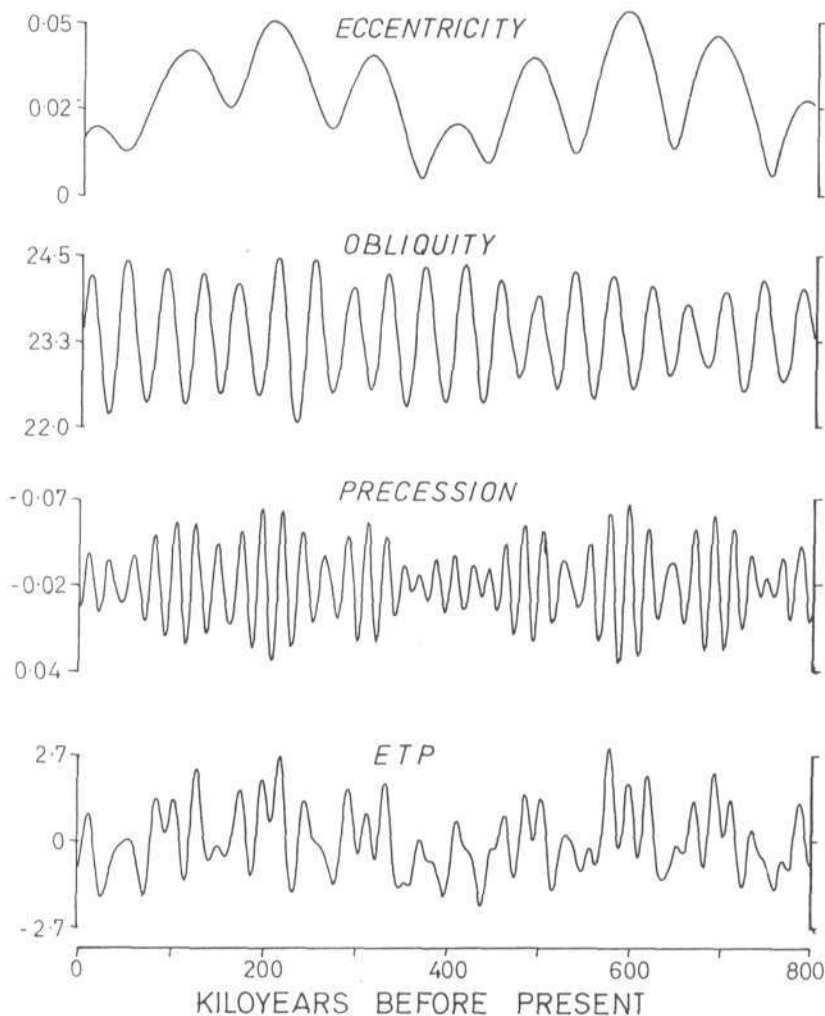


Figure 2.6 Precession, Obliquity and Eccentricity Cycles

different climatic zones through time. There are two main Eccentricity Cycles (106,000 and 410,000 years) relating to changes in the shape of the earth's orbit around the Sun from near-circular to elliptical, and in the periodically eccentric position of the Sun in relation to the orbit. All this was used by Milankovitch to calculate the complicated net result of these effects and how they might explain the history of ice ages.

The summation of the energy reaching the earth from the Sun, as a result of all these changes in the orbital pattern, could appear to be

very irregular and complicated, since it summates several different oscillations; but, as with the Fourier transform discussed earlier, the controls may be basically simple. Thus we have a series of orbitally controlled oscillations affecting the earth's environment, from tidal up to the galactic year. This gives us a remarkable potential for establishing very detailed time-scales for the geological past.

I would like to draw attention to a particular problem of the climatic interpretation. Unfortunately we do not, as yet, have time-scales which might enable us to say whether the mid-Palaeozoic black shale events are periodic or that there are equal times between them, and hence that they may be climatically controlled by orbital factors. Hopefully within a few years, work on fitting periodicities to the Milankovitch orbital change effects – the orbital forcing time-scales (OFT) – with a precision down to 20,000 years, may provide a tool to enable us to do this. In recent years there has been a growing view that these do not represent peaks of cold, as in the ice ages, but peaks of heat, and a climatic cyclicity is the driving force.

The emphasis on extra-terrestrial causes (House, 1995) for many environmental changes should not detract from the importance of earth-bound causes. Mountain building and ocean ridge activity have important episodic effects on sea level and climate. Tsunami, earthquakes and volcanism are other violent events with complex attributes. The combination of extra- and endo-terrestrial events means that environmental change gives a continuously varying background control to evolution.

It seems to me far too simplistic to view evolution as merely stasis versus punctuation as Steve Gould has done. Nor would I accept the view of Chris Paul (Chapter 1) that 'Stasis is the norm' or 'Stasis rules, OK?' For stasis referring to taxa I think it still has to be demonstrated that the majority of taxa are long-lived: for the ammonoids quite the reverse is documented in Figure 2.3, where the left-hand peak shows that extinction of short-lived genera is the greatest. Stasis in relation to the environment, on the other hand, is even less convincing, since there is a gradation from short-term local stress events, such as a high tide, or tropical storm, which might extinguish individuals, right up to the major paroxysms of Deccan Trap volcanism and its ocean ridge association, and the meteorite impact of the K/T boundary which extinguished orders and families. Even the Devonian extinction events listed in Figure 2.1 differ in their effect, the greatest being the Taghanic, followed by the Kellwasser, Hangenberg and others, with decreasing importance.

I have highlighted these developments for two reasons. Firstly to show that the fluctuating environmental contingency factors are

important in ensuring there is no such thing as environmental stasis: flux is part of the nature of the environment of evolution. It would follow from this that evolutionary stasis would be unlikely also, at least as a generalization. Some taxa, with wide tolerance, assured habitat and food supply, are likely to show stasis, but most may not be so lucky. Secondly, the possibility of a new type of OFT may provide great precision for geological history in the same way that other expressions of orbital forcing (through giving rise to varves and dendrochronology), have in the relatively recent past.

All this brings us back very directly to those classic theories of punctuated equilibria introduced by Eldredge and Gould (1972) and Gould and Eldredge (1993), which suggested that evolution consisted of episodic radiation events separated by evolutionary stasis. If my thesis here is correct, then environmental changes, and with that evolutionary changes controlled by the environment (which most are), will be in a continuing state of flux, occasionally giving exceptionally high stress with associated major extinctions, but always exerting some control on extinction and the organic world.

Conclusions

The significance of all that I have discussed for the debate on evolution is to show that there has always been change in that major contingency factor which controls evolution, the environment. And we are only just beginning to understand some of the causations. If there is no environmental stasis, then there is unlikely to be any for evolution, and the punctuated evolution model falls. Nevertheless the remarkable thing about the new high-resolution stratigraphy which is being developed is the way in which evolutionary events can be documented not only precisely in time, but also – through the improved techniques for correlation – the events can be documented on a worldwide scale. Thus much of the present verbiage on past views on evolution, the history of ideas, and the speculation and argument over processes, will be replaced in the years to come by arguments based on primary data of an incredible time precision.

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3 Pattern and process in hominid evolution

Robert Foley

Summary

Explanations in evolution generally, and human evolution in particular, vary in the extent to which emphasis is placed on adaptation or on other factors, such as chance or historical contingency. In this paper the broad pattern of hominid evolution above the species level is described and used to throw light on the processes of evolution involved. Adaptive radiations, species survivorship, biogeographical patterns and the relationship with climatic change all show that chance and historical contingency play a role in the formation of the initial conditions under which evolution occurs, but that the detailed micro-evolutionary shape of any outcome is a function of adaptation and selective mechanisms.

Introduction

The development of the theory of natural selection and the widespread acceptance of evolution in biology is usually treated as a watershed in biological thought. As has often been discussed (Bowler, 1989), the innovation of Darwin and Wallace was not so much the proposal that evolution had occurred, but their specific mechanism for accounting for its occurrence and pattern. That theory – differential reproductive success leading to changes in gene frequencies resulting in better adapted organisms and populations – tipped the balance of a long-standing debate over

what shapes plants and animals. Darwin placed the emphasis on function, hence the key role of adaptation in neo-Darwinist theory; organisms are the way they are because of the requirements of their environment, through the mechanism of natural selection.

Historically, alternative theories placed the stress on other factors. One such was the idea of archetypes, which in modern biological terms equates to the constraints of structure and development: organisms are the way they are because there are only a limited number of ways in which 'biological design' can be implemented. The rise and triumph of Darwinism has not necessarily seen the disappearance of all other factors in evolution other than natural selection. Indeed, debates within evolutionary biology revolve primarily around the relative significance of natural selection and the way in which this mechanism interacts with others. The primary alternative candidates remain much the same as in the nineteenth century (see Gould's Introduction, p. xiv) — the constraints of development on adaptive design, and the effect of past events — 'history' on subsequent evolutionary pathways. It is these factors that make evolutionary events, and the operation of natural selection, contingent. The question that arises for human evolution, therefore, is the significance of contingency in the evolution of one particular lineage. More specifically, how can we balance explanations that stress function in evolution, and those that stress contingent factors. Here I shall look at the overall pattern of hominid evolution to see what can be inferred about process, and in particular the relative roles of adaptation and other, more contingent, factors.

Species in human evolution

A first problem that arises is the extent that human evolution is a single lineage. Conventionally, since the more rigorous application of the rules of zoological nomenclature and the widespread acceptance of the biological species concept, human evolution has largely been treated as anagenetic in character, involving a limited number of taxa, and consisting primarily of an expansion in the size of the brain. Much of the rest of palaeoanthropology could largely be considered to be concerned with the minutiae of anatomy.

It is clear that this is no longer the case. When Mayr (1950) pruned the human evolutionary tree he reduced it to three basic species — *Australopithecus africanus*, *Homo erectus* and *Homo sapiens*, with a possible fourth in the form of a more megadontic species, *A. robustus*. Since that time there has been a steady upward drift in the number of recognized hominid species. Pilbeam's (1972) widely read synthesis added *H. habilis* and gave stronger credence to the

robust australopithecine. Howell (1978) split the robust australopithecines to add further taxa, resulting in eight. Groves (1989), using a formal phylogenetic analysis, proposed sixteen species, while a recent survey by Wood (1991, 1995) suggested thirteen species. Foley (1991) argued that there were a maximum of nineteen known species in the hominid fossil record.

This increase in taxonomic diversity among the hominids has been partly a result of the relentless discovery of new species of hominid, of which *Ardipithecus ramidus* is but the most recent (White et al., 1994), principally in Africa, over the last three decades. It has also been affected by the increased use of cladistics, which both requires more species for analysis to be possible, and depends on defining taxa at the outset of the analysis. Where multivariate statistics tended to stress overlap between hominid morphologies, cladistics works best by emphasizing differences.

Now the rise in the number of taxa is significant because it means we are not dealing with a straightforward anagenetic or simple linear evolutionary process, and therefore we can start to compare different hominid species. Evolutionary biology is essentially a comparative subject, and having several species allows the comparison of different hominids adaptively as well as simply in terms of gradual transitions from one to another. Each of these species will have a specific point of origin, time of last appearance, and by calculation, a longevity or duration – the time elapsed from appearance to disappearance. This type of data (Figure 3.1) allows us to talk about more general evolutionary processes – extinction and speciation – in ways that are comparable with palaeontologists and evolutionary biologists working on other lineages distant from humans.

Hominid evolution as a pattern of adaptive radiations

The advantage of treating hominid evolution as a constellation of species, rather than an evolving lineage, is that we can ask what are the causes of evolutionary change in general, the patterns and processes of human evolution. What causes speciation and extinction? How long do hominid species survive? What are the patterns of diversity? Do hominid species coexist and if so, how do they interact? This last question is important in broad terms, for it is an area for which we have few models. *Homo sapiens* is the sole surviving species, and so we know little about the way in which a human or hominid would interact with a closely related species.

The first such observation is that, with the multiple species and contemporary species observable in Figure 3.1, the pattern of

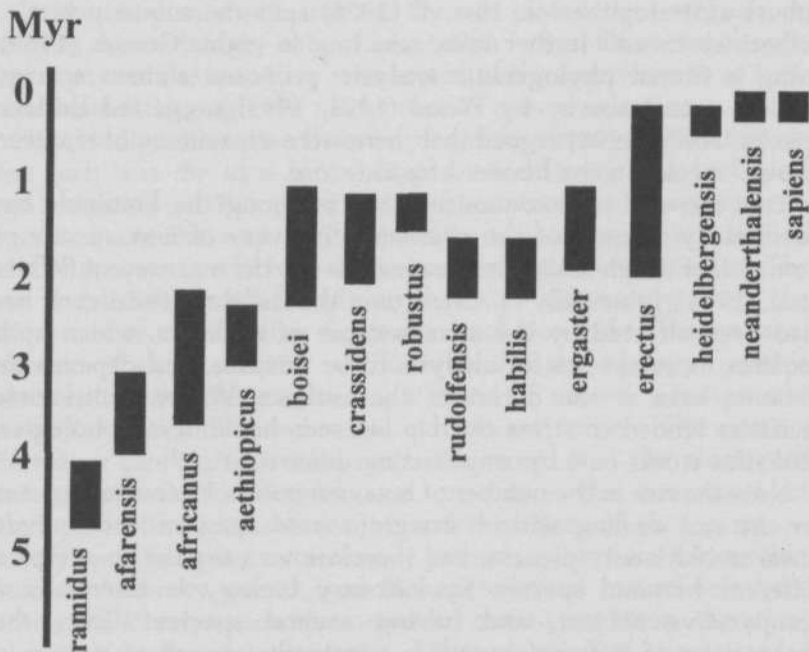


Figure 3.1 Species in human evolution

hominid evolution can be described as a series of adaptive radiations. An adaptive radiation is when there is a diversification of lineages from an ancestral lineage – in other words the multiplication of closely related taxa, usually linked by a common set of characteristics and adaptations. Three such radiations can generally be recognized (Figure 3.2): that of the early bipeds from around 4 Mya (*A. ramidus*, *A. afarensis*, *A. anamensis*, *A. bahrelgazali*, *A. africanus*); that of the megadontic robust australopithecines (*A. aethiopicus*, *A. boisei*, *A. robustus*, *A. crassidens*); and that of the more encephalized *Homo* (*Homo habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, *H. rhodesiensis*, *H. heidelbergensis*, and *H. neanderthalensis*). A fourth is shown here – the spread of *Homo sapiens* (AMH), but this is fundamentally different in not involving biological diversification to anything like the extent seen in the other ones. The radiation of *Homo sapiens* is one of geographical dispersal, and is significant for its behavioural implications.

In terms of the processes of evolution involved, the occurrence of multiple species within the hominids and the pattern of adaptive radiations is significant in that it conforms to that found in other groups of animals. Adaptive radiations are the norm of

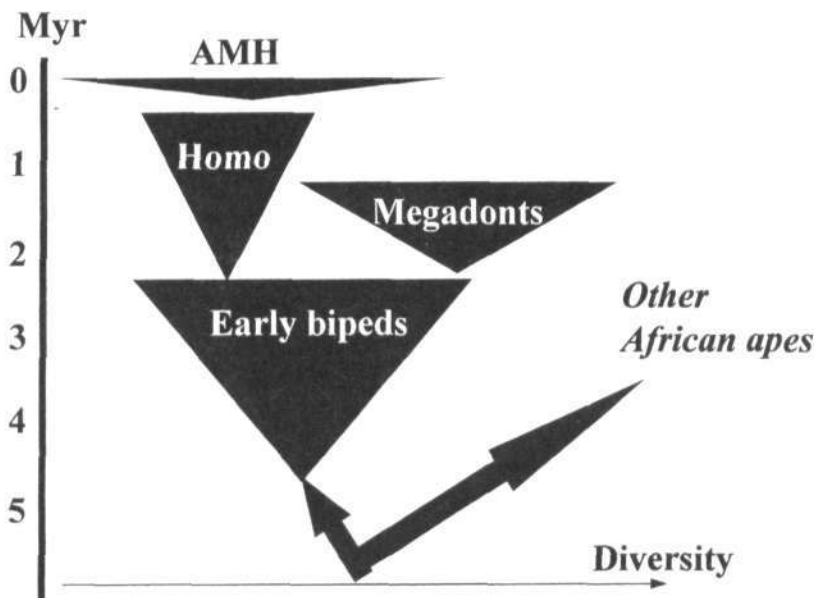


Figure 3.2 Hominid evolution as a pattern of adaptive radiations

evolutionary biology. New forms evolve, and then radiate and diversify to fill a range of ecological niches and geographical positions, and then they will gradually dwindle and decline through extinction, resulting in a loss of diversity. The shape of hominid evolution is the same as the shape of that of any other group, and there is nothing very special at this level (Foley, 1987, 1995b). It might therefore be possible to infer that the mechanisms and processes underlying hominid evolution are not qualitatively different from those of other species.

What of the roles of adaptation and more contingent factors in these adaptive radiations? In one sense they are clearly the result of contingency: the evolution of bipedal apes in Eastern Africa five million years ago is contingent upon the effects that rifting activity had upon the climates of Africa, and contingent upon the presence of large-bodied suspensory hominoids in adjacent or relict arboreal habitats. The geographical radiation of *Homo* was contingent upon the climatically determined shifts in both sea level and habitat distributions. Different abiotic and phylogenetic circumstances would undoubtedly have produced different evolutionary outcomes. However, while the timing and location of evolutionary events may be contingent upon the historical situation, it is clear

that the way in which the evolutionary responses are played out is a function of other mechanisms. It is here that the role of natural selection becomes clear. Given certain initial conditions, the outcome will be the product of competitive interactions between individuals, populations and species, in which those organisms best suited to the conditions will have a reproductive advantage. In this way characteristics such as bipedalism or increased meat-eating, characteristics that underlay the hominid adaptive radiations, are adaptive, functional, and the product of natural selection.

The survivorship of species

From the ten or more species of hominid that have existed, only one is still in existence. The unitary nature of the human species is itself an interesting problem, as is the question of when hominids last occurred in multiple species. However, from the point of view of the pattern and process of hominid evolution, one useful approach is to consider how long hominid species survive. Is it a matter of chance which species survive, and which ones become extinct? Are there patterns to survivorship within the hominid lineage? Using Gould's (1989) metaphor, were the tape to be replayed, would the outcome be the same, or would the Neanderthals have replaced modern humans, or the robust australopithecines survived through to the present day, where we might watch them chewing away in London Zoo? Certainly it is an interesting observation, since two million years ago the robust australopithecines appear to be far more abundant in the fossil record than early *Homo* (Wood, 1991).

The average longevity of a mammalian species is around one million years (Stanley, 1978). Species longevity can be very crudely estimated by subtracting the date of last appearance in the fossil record from the date of first appearance. When this analysis is carried out for hominids, it appears that the average longevity is close to the mammalian average of one million years (Foley, 1993). Again, this supports the view that hominid evolution, in pattern at least, is similar to that of other mammalian groups. The average duration, however, hides considerable variation. Some taxa, such as *Australopithecus africanus* and *A. afarensis* have longevities that exceed one million years, while the 'species' of *Homo* are all rather short-lived. Our own species, *Homo sapiens*, has been in existence for little more than 100 kya, and Neanderthals lasted as a species for not much longer than this.

This variation may tell us something about pattern and process. One observation is that species turnover increases during the course of hominid evolution. The tempo of evolutionary change is

accelerating. This may be due to a number of factors – the increased rate of climatic change (but see below), or the autocatalytic effect that human behaviour had on evolutionary rates, or the greater diversity of habitats occupied as hominids became more global in distribution. However, it may also be the case that what is taken to be a species becomes increasingly suspect in the later parts of human evolution, and therefore the results are an artefact. Even artefacts are interesting, though, and the problematic nature of the species concept in later human evolution might be itself an indication of a changing set of processes – a greater role for behavioural mechanisms or the relatively rare problems associated with pan-global distributions.

In terms of inferring process, a study of species survivorship is informative. Perhaps the most interesting point is that while at the level of the family as a whole there are regularities that lead to hominids converging on the mammalian mean, each of the events underlying it is a response to unique conditions and chance events. In other words, if several factors are operating – and they may be contingent, stochastic or strongly deterministic and functional – the macro-patterns will not reflect the variability in the underlying causes. Macro-evolution will not reflect micro-evolution (see Paul, this volume).

The geography of hominid evolution

If we accept that hominid evolution is not a simple linear process, the ladder of progress up towards modern humans, but actually a series of adaptive radiations, then one of the implications is that the hominid lineage has undergone speciation, that new species have arisen. This observation takes us into one of the most controversial areas in evolutionary biology – what promotes speciation? Under what conditions do new species arise? Do new species always arise through cladogenesis? Rather than pursue the complexities of speciation theory here, I will look at the patterns of speciation among the Hominidae, to see if this can throw light on the conditions under which new hominid taxa have emerged.

A starting point might be the patterns of speciation found in non-human primates. The catarrhines (Old World monkeys and apes) show a clear trend – where a genus is distributed over a large area, there will be a large number of species. In other words, new and more species will occur as geographical range increases (Foley, 1991). This is consistent with an allopatric model of speciation: as populations disperse, and cover a larger area, a greater number of geographical barriers, or other barriers to reproduction, start to occur; in addition adaptation to different environments will

promote differences between populations. Divergence – or speciation – is a response to geographical dispersal.

If we look at hominid evolution in geographical rather than chronological terms, we can use models derived from the catarrhines to see whether new hominid species occur in response to geographical dispersal in the same way as other catarrhine species.

The details of this analysis have been presented elsewhere (Foley, 1991). The principal points that emerge are that during the earlier part of hominid evolution, that is when the australopithecines and early *Homo* occurred only in parts of sub-Saharan Africa, the number of species observable in the fossil record (between 6 and 10) conforms to the number predicted by the catarrhine model. Speciation among early hominids is both relatively common and occurs at about the rate that would be expected for an ape. However, as hominids expanded out of Africa between two and one million years ago, the number of taxa did not increase markedly. The model would predict more than 20 species of later Pleistocene hominid, whereas even the most rampant splitter is unlikely to recognize more than four or five, and two or three is far more probable. For later hominid evolution, patterns of speciation do not fit the primate-based model, and one might infer that different mechanisms are occurring.

A further comparison is illuminating here. Other groups have very low rates of speciation in response to broad geographical distributions, of which the best examples are the large carnivores. Not only does the species concept not work very well for these groups, as was the case for later hominid evolution (see above), so too it appears that they are able to disperse very widely without speciation.

In other words early hominids are speciating like typical catarrhine primates, but later hominids are behaving more like carnivores. What does this tell us in terms of evolutionary process? Two points should perhaps be highlighted. The first is that if we think about why geographical dispersal should lead to speciation, the answer lies in the formation of geographical barriers, separating parent and daughter populations. Such barriers are usually (although not exclusively) abiotic, and thus the conditions for speciation are independent of the vectors of selection. Contingency – unpredictable initial conditions – therefore underlay the fundamental mechanisms of evolutionary divergence. The second point, however, is in contrast to this. Both primates and large carnivores have dispersed widely and met barriers; their response, though, has been very different. The differences are due to the

adaptive differences between the groups – carnivores are more tolerant of resource and habitat variation than the primarily herbivorous primates. Once again response to novel circumstances, therefore, is strongly influenced by initial conditions which are partly stochastic, but the final outcomes are the result of strongly deterministic forces. In hominid evolution it appears that there is a change in those deterministic forces – selection – that occurs in later hominid evolution, possibly as a response to increased meat-eating, that affects the pattern of subsequent hominid evolution.

Climate and hominid evolution

The interaction between biotic and abiotic, stochastic and deterministic, adaptive and historical factors that has underlain this discussion of processes in human evolutionary biology, has been tangentially tackling the issue of causality in evolution. A related issue is whether evolution is dependent upon external environmental change, or whether there is a purely biological dynamic involved. The testing ground for this debate is the relationship between climatic change and human evolution. Why do particular species appear at particular times? Is it a product of climatic change?

The most powerful model for a driving force in hominid evolution is a climatic one. Vrba (1985) suggested a relationship between the split from *Australopithecus* to *Homo* and the climatic deterioration that occurred at around 2.4 million years. Suggestions for other climatic events, such as one affecting the origins of *H. sapiens*, have also been made. These are particular events in hominid evolution, but now that a large number of taxa have been identified it is possible to develop a quantitative test of the more general proposition that climatic change is a necessary cause of speciation. Again, the results of these analyses have been presented elsewhere (Foley, 1994); here it is the general implications that are significant. The primary finding of an examination of the relationship between hominid and baboon speciation and climatic change in a number of variables (average temperature, climatic stability, etc.) showed no significant effect. Even when extended to other mammalian groups, the only species that seemed to be directly sensitive to climatic change were the African bovids. This remained true at different scales of chronological resolution and temporal lagging. While there is no relationship between the appearance of new species and climate, there is a weak one between climate and extinction.

The conclusion to be drawn is that climate does not directly drive evolutionary change. Evolutionary change can occur without any climatic change, and equally climate can change without any

apparent evolutionary effects. Again, the pattern of hominid evolution can throw light on the processes. It appears that external environmental change has the most direct effect on rates of extinction. This is much as would be expected, through such mechanisms as habitat loss and fragmentation. How new taxa respond through evolutionary change and speciation, though, is subject to a far greater number of factors. The link is far more indirect, and in particular local demographic and competitive conditions are bound to play a major role. Once again, to understand evolution it is necessary to return to the small scale and the local, and there the role of selection, competition and adaptation is likely to be significant. Evidence for this view is perhaps to be found by looking at what is actually evolving among the hominids. There is increasing evidence that during early hominid evolution at least there was considerable parallel evolution – that is, the same characteristics evolved independently in more than one lineage. Megadonty, for example, the key trait of the robust australopithecines, may have evolved three times (Skelton and McHenry, 1992) and Wood (1991) has shown that homoplasies are rife in the early hominid evolutionary record. Convergence is perhaps the strongest evidence for adaptation, and indicates that despite the contingent factors that lie at the base of evolutionary episodes, the rules of survivorship and reproductive success govern the final outcome (Foley, 1995a).

Conclusion

A number of general points have been made about the processes underlying human evolution on the basis of the pattern that we can observe in the fossil record. The first of these was that the pattern of hominid evolution is similar to that of other mammalian lineages, and therefore it is likely that the mechanisms are similar too. The second was that while contingency plays a part in the timing and location of evolutionary events, the way those events are played out, the final biological outcomes, are strongly influenced by selection, adaptation and function. In this sense discussions about the roles of selection versus other factors in evolution will relate not so much to competing explanations, but to explanations of different phenomena. Contingency helps us to set out the initial conditions under which evolution occurs, natural selection provides us with the rules governing responses in the evolving populations. The third was that macro-evolutionary patterns will tend to disguise the variability in process that occurs in micro-evolution. By stressing the overall pattern, we have lost sight of the significance of

selective mechanisms as well as the details of the contingent events. Macro-evolutionary approaches cannot be a substitute for looking at the details of micro-evolution.

Gould, in his Introduction, has suggested that the history of evolutionary thought can be represented as a triangle of mechanisms underlying explanations of evolutionary change – adaptation, historicity, and chance. Different schools of thought might place variable emphasis on these, although all would recognize that each must play a role. However, in considering the patterns and processes of hominid evolution, the insight that has emerged most strongly is that these factors are not competitive, but complementary, and that evolution is the outcome of both stochastic and deterministic processes. As such, should the tape of life be replayed, undoubtedly there would be many differences, but there would also be a very significant number of similarities.

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4 Contingency, patterning and species in hominid evolution

Alan Bilsborough

I am fully convinced that species are not immutable; Furthermore, I am convinced that Natural Selection has been the most important, but not the exclusive, means of modification (Darwin, 1859)

... the embodiment of contingency: *Homo sapiens* is an entity, not a tendency (Gould, 1990)

... punctuated equilibrium is a claim about relative frequency, not exclusivity (Gould and Eldredge, 1993)

Summary and introduction

Over the last two decades palaeobiology in general has been much influenced by debate about the nature of evolutionary processes, species characteristics, and the form and significance of patterns discernible in the fossil record. In particular, the explication of punctuated equilibria (Eldredge and Gould, 1972) as an alternative evolutionary model to phyletic gradualism has stimulated consideration of the nature of species, of speciation mechanisms and of extinctions, and the significance of evolutionary trends. Unlike phyletic gradualism, the new evolutionary paradigm views macro-

evolutionary phenomena as something distinct from the mere cumulative effects of micro-evolutionary processes, so requiring separate explanation. Random factors and contingent events can play major roles in such interpretations, particularly in the origin of species, and in their persistence or extinction: the phenomenon described as species selection (Stanley, 1979) or species sorting (Eldredge, 1995).

Although touched by these developments, hominid studies have been less influenced than many other areas of palaeontology, and certainly less than might have been expected. Nonetheless, there has been a corresponding, albeit more limited, conceptual shift within palaeoanthropology towards multiple species recognition, and therefore more frequent extinctions, among fossil hominids. However, in my view this has more to do with the enhanced diversity revealed by the now much expanded early hominid fossil record, and the recent vogue for cladistic analysis, than the stimulus provided by the conceptual developments in palaeobiology referred to above.

Punctuacionists view impeded gene flow among peripheral or otherwise isolated populations as the main engine powering speciation, itself the primary source of the diversity revealed by the fossil record. Recent developments in palaeoanthropology have led some workers to argue for an early (terminal Pliocene) and widespread dispersal of hominids out of Africa to Europe, central Asia, the Far East and Sundaland. Such occurrences, if confirmed, would clearly enhance the possibilities for speciation and for contingent events having significant influence in human evolution.

In this paper I therefore summarize some aspects of hominid phylogeny and the patterns revealed by the hominid fossil record, and attempt to assess the possible role(s) of contingent factors in influencing those patterns. There is an obvious difficulty here. Few would dispute some role for stochastic factors in hominid evolution, particularly at the local level, but in this context the effects need to be significant enough to affect outcomes at the macro-evolutionary (species) level – the second tier of Gould (1985). Outcomes resulting from chance events can never be identified with certainty; apparent instances may be as much (or more) to do with the incomplete nature of the evidence (see Paul, House, this volume), or the inadequacy of our analysis rather than representing 'real' phenomena. There is consequently a danger that in identifying examples of contingency in human evolution we are doing nothing more than formalizing ignorance, and this needs to be borne in mind throughout what follows.

In addition we all bring a good deal of intellectual baggage to our interpretations of the fossil record. My own perspectives on

this (e.g. *Bilsborough, 1992*) have developed predominantly within the framework of a neo-Darwinian interpretation of evolutionary processes, and an associated gradualist model of phyletic change. A major corollary has been that my preferred phyletic schemes have been strongly adaptationist with the minimum number of clades and species judged compatible with the evidence, and with a tendency to identify and stress trends, and so allow little role for contingent factors. Other workers (e.g. *Groves, 1989; Tattersall, 1986, 1992, 1995; Foley, 1995, this volume*) have happily identified many more species, and correspondingly more extinctions, on the basis of the same evidence. Some (e.g. *Tobias, 1991; Wolpoff et al., 1994*) would recognize fewer than I do. (See *Fig. 4.1a-f.*)

In light of these difficulties and subjectivities, how best to proceed? Given the punctuational view of the fossil record as unbiased – i.e. as complete and representative at one time as at any other, and an equally faithful reflection of different evolutionary phenomena – it seems appropriate to focus on morphological discontinuities in the record as potential indicators of speciation and extinction, and to consider the extent to which contingent effects might be significantly implicated in these. In this article I therefore attempt to identify discontinuities in the relevant fossil record and interpret them in terms of what I understand to be the main features of the punctuational model. However, quite apart from the imperfect nature of that understanding, conceptual bias undoubtedly remains, and needs to be watched for in what follows.

In the following sections I initially summarize some relevant aspects of hominid morphological diversity within a chronological and continental framework, and for the reasons referred to above, I also review in some detail evidence for the proposed early entry of hominids into Asia and Europe. I then attempt to identify examples of macro-evolutionary phenomena, and the environmental and ecological backgrounds to these. Following a summary of such instances, I then suggest possible mechanisms to account for these, and the role of contingency in such processes. I hope that this 'bottom up' approach will usefully complement *Foley's* survey (*Chapter 3*), which adopts an alternative, comparative, perspective and analyses hominid evolution in terms of patterns derived from the record of mammalian evolution in general.

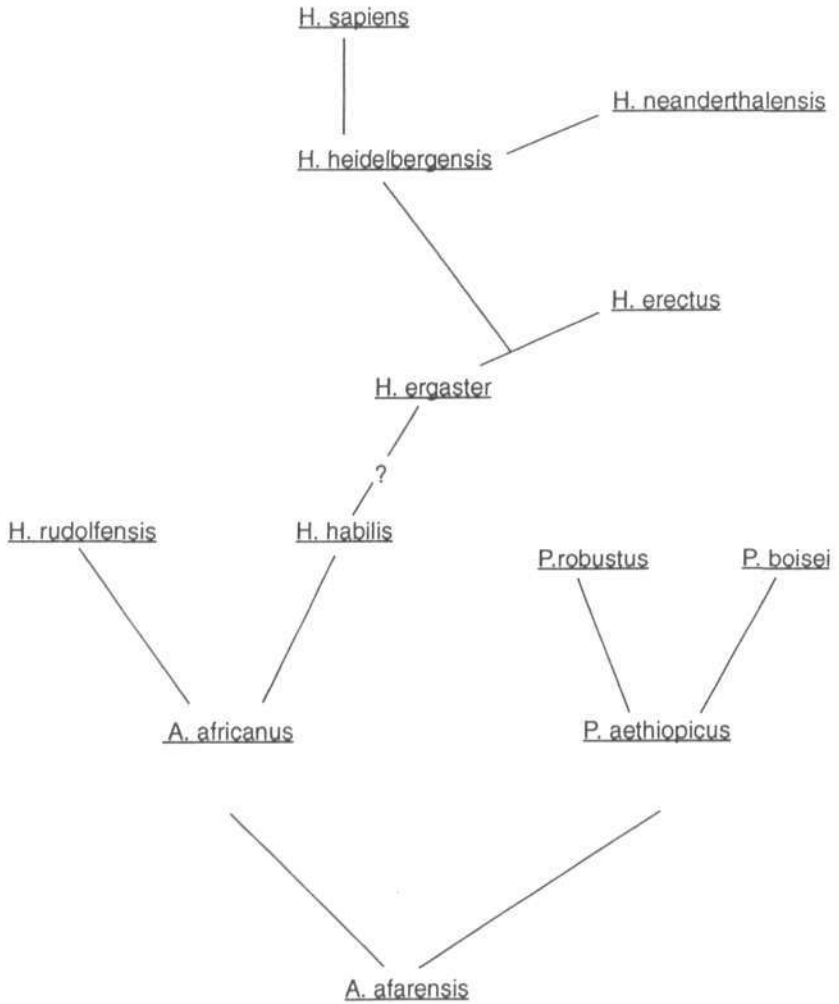


Figure 4.1a An interpretation of hominid phylogeny: Tattersall (1995)

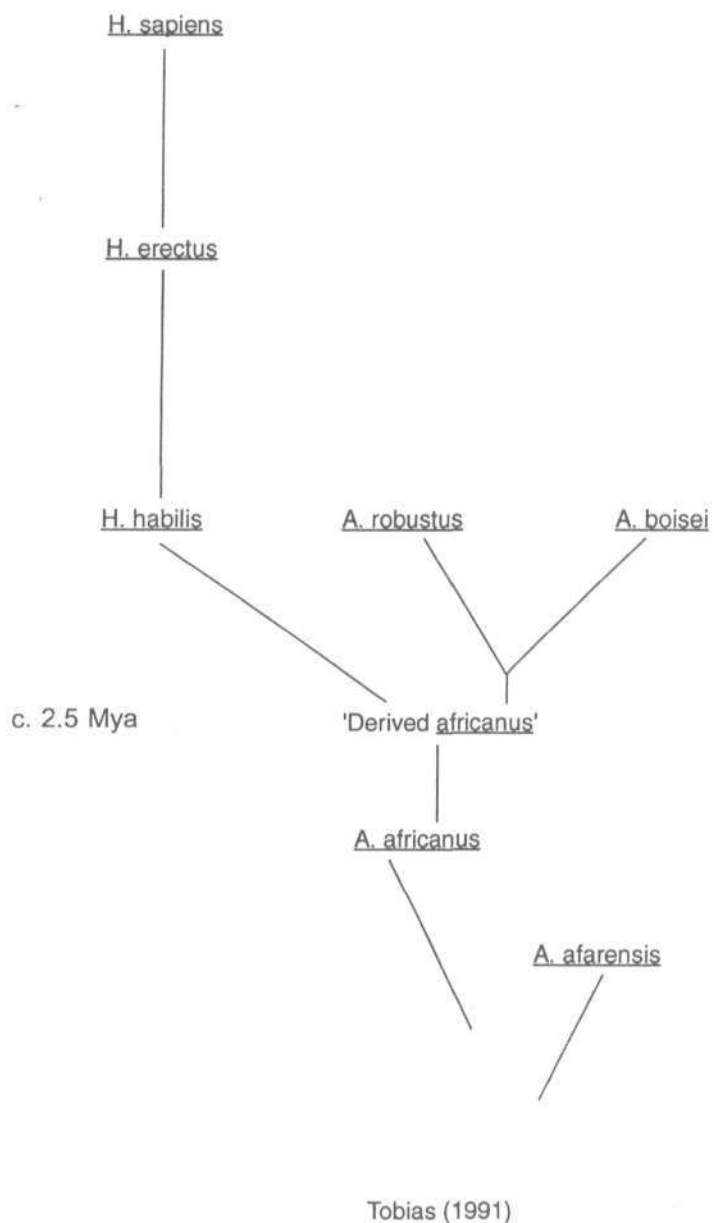


Figure 4.1b An interpretation of hominid phylogeny: Tobias (1991)

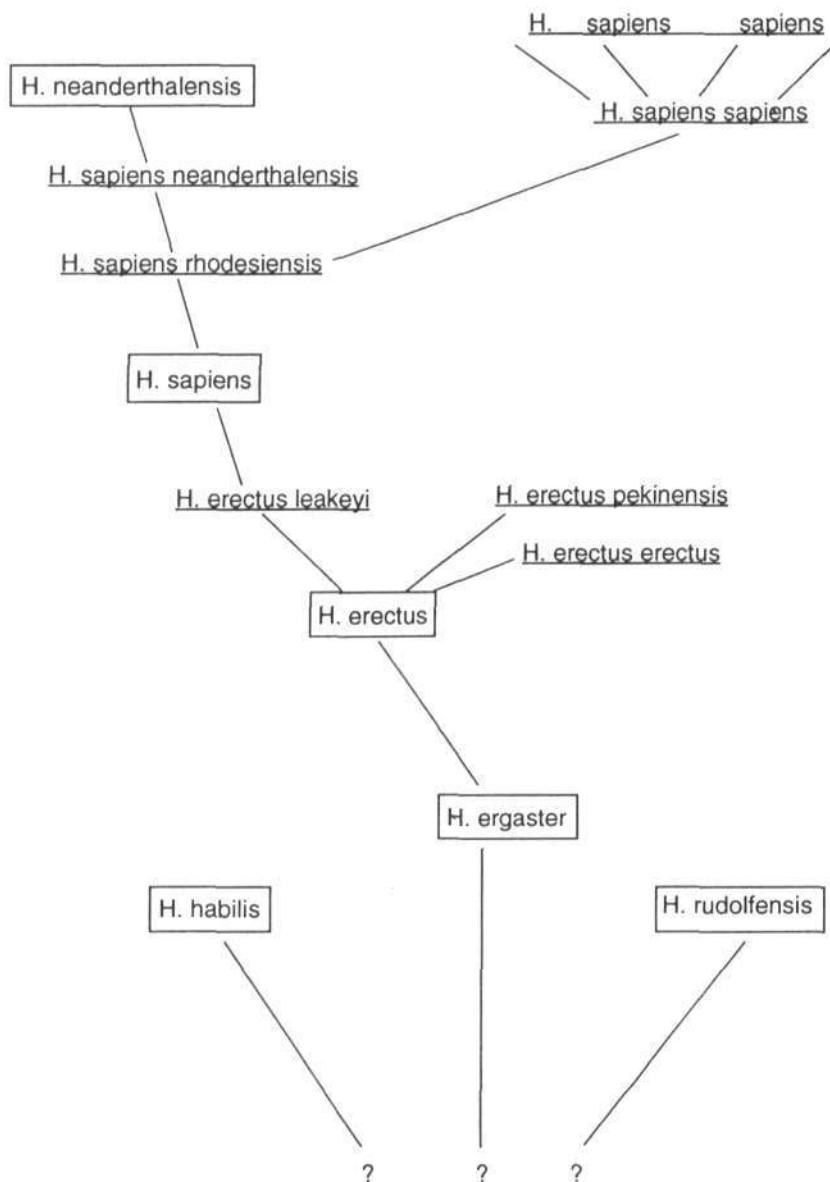


Figure 4.1c An interpretation of hominid phylogeny: Howells (1993)

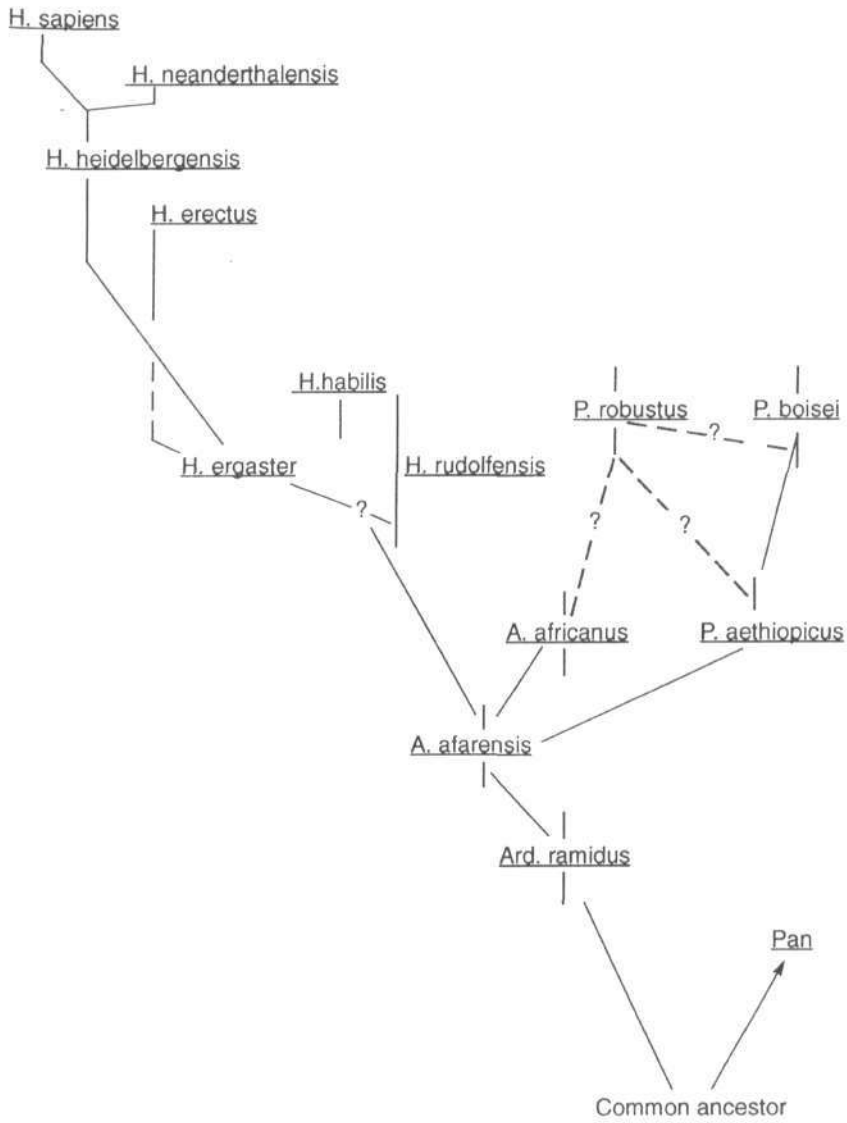


Figure 4.1d An interpretation of hominid phylogeny: Wood (1994)

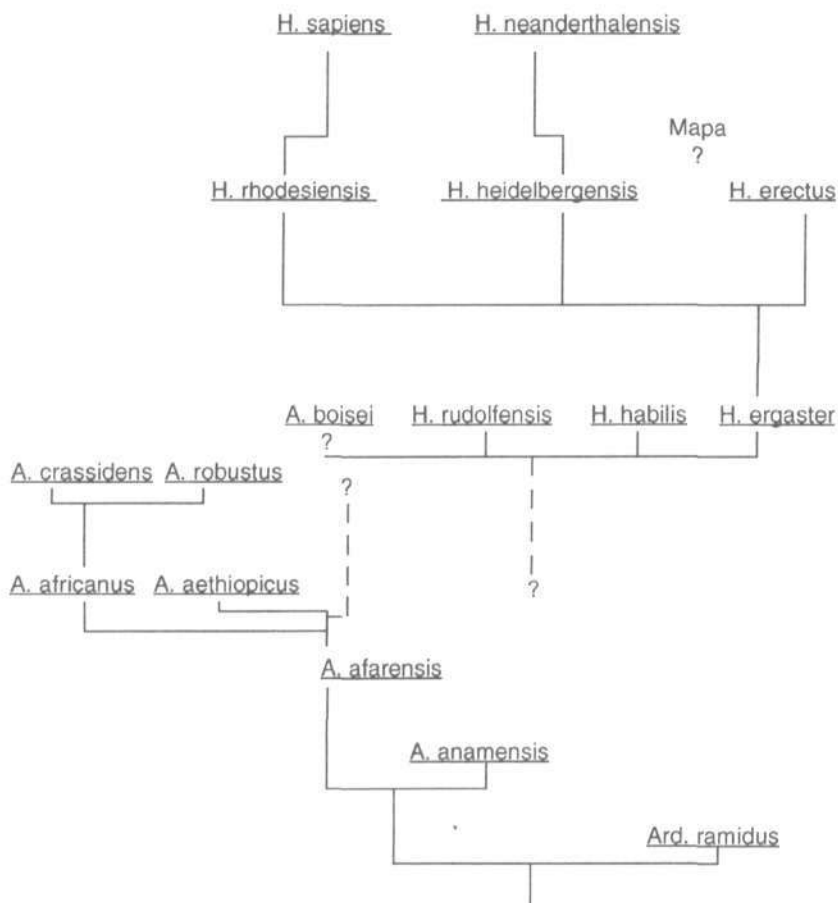


Figure 4.1e An interpretation of hominid phylogeny: Foley (1995)

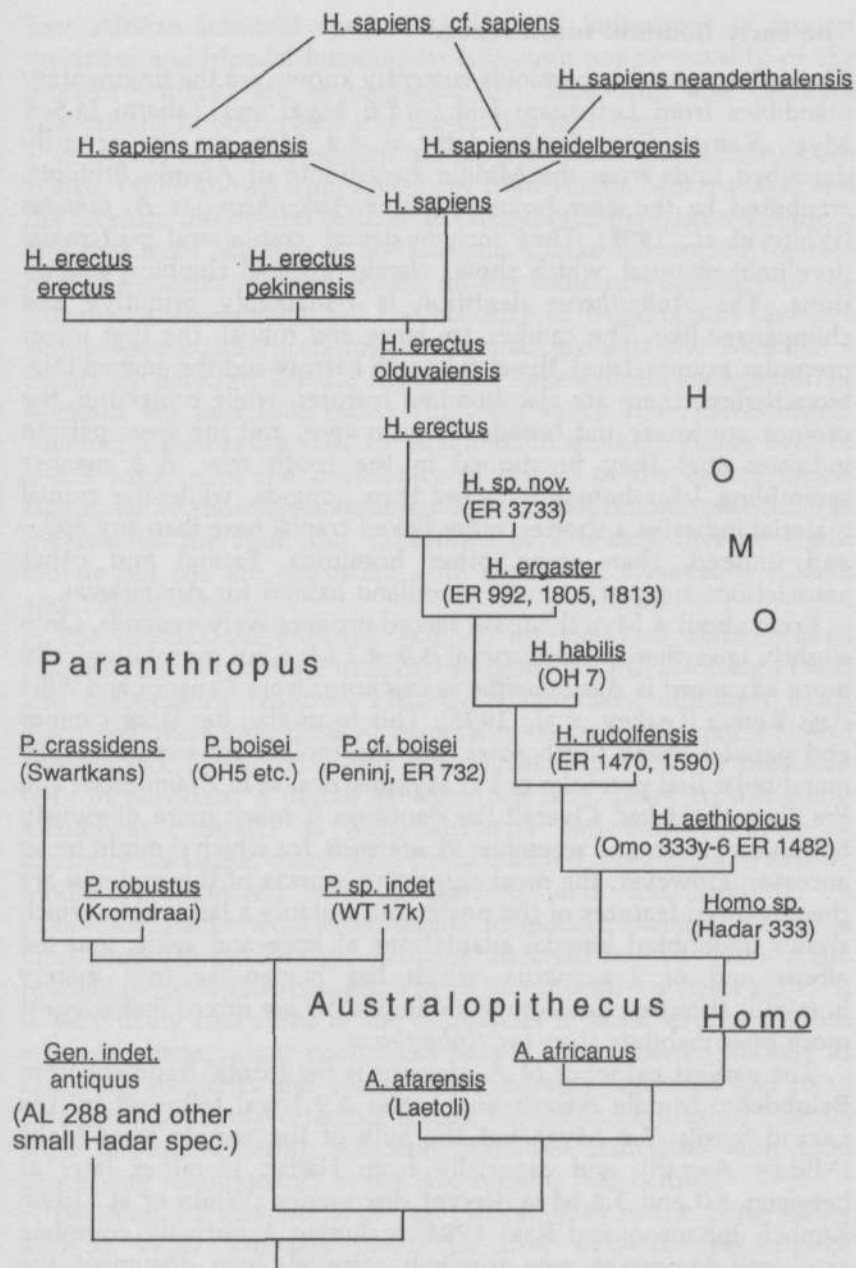


Figure 4.1f An interpretation of hominid phylogeny: Groves (1989)

The early hominid fossil record

The earliest possible hominids currently known are the fragmentary mandibles from Lothagam Hill (> 5.6 Mya) and Tabarin (4.5–5 Mya), Kenya. Considerably later at 4.4 Mya are the recently described finds from the Middle Awash site of Aramis, Ethiopia, attributed to the new hominid genus *Ardipithecus* as *A. ramidus* (White et al., 1995). They include dental, cranial and postcranial (forelimb) material, which shows clambering and climbing adaptations. The *Ardipithecus* dentition is remarkably primitive and chimpanzee-like. The canines are large and robust, the first lower premolar asymmetrical, the cheek teeth narrow and the enamel thin. Nonetheless, there are also hominid features: while projecting, the canines are lower and broader than in apes, and the wear pattern indicates that they functioned in the tooth row in a manner resembling later hominids rather than pongids, while the cranial material indicates a shorter, more flexed cranial base than any ape – and, indeed, than some other hominids. Faunal and other associations suggest a closed woodland habitat for *Ardipithecus*.

From about 4 Mya the fossil record progressively expands. Only slightly later than *Ardipithecus* at 3.9–4.2 Mya but morphologically more advanced is *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya (Leakey et al., 1995). This form also has large canines and parallel cheek tooth rows, but the molars are expanded, the mandibular first premolar not as asymmetrical as in *Ardipithecus*, and the enamel thicker. Overall the dentition is much more obviously hominid in form, and resembles *A. afarensis*, for which it might be an ancestor. However, the most surprising aspects of this material are the advanced features of the postcrania, notably a large tibia, which shows undoubted bipedal adaptations at knee and ankle, and the elbow end of a humerus, which has human-like (not merely hominid) affinities. Environmental indicators are mixed, but suggest more open habitats than for *Ardipithecus*.

The earliest evidence of *A. afarensis* is the frontal fragment from Belohdelie, Middle Awash (just under 3.9 Mya) followed by the Laetoli fossils (3.6 Mya), but the bulk of the sample from Maka (Middle Awash), and especially from Hadar, is rather later at between 3.0 and 3.4 Mya. Recent discoveries (White et al., 1993; Kimbel, Johanson and Rak, 1994) including a virtually complete skull and important new forelimb material, help document the characteristics of this early hominid species. They confirm the essential accuracy of the original descriptions, and of the characterization of *afarensis* as a single, but strongly sexually dimorphic and therefore highly variable, and widely distributed,

East African hominid species. Undoubted indications of trunical erectness and bipedal locomotion (although not necessarily of the modern variety) are accompanied by clambering and climbing adaptations in both small and big-bodied individuals.

A similar pattern is evident in the *A. africanus* fossils from South Africa. While known from specimens from Taung, Makapansgat and the recently discovered teeth from Gladysvale, the largest sample is still that from Member 4, Sterkfontein. Clarke has argued for two hominid species at Sterkfontein on the basis of variability in the Member 4 assemblage, but the majority of workers still favour a single species interpretation. On faunal grounds the Member 4 fossils are dated to 2.4–2.8 Mya, but Clarke's recent recognition of hominid leg and foot bones from the much older Sterkfontein Member 2 pushes the date for hominids in southern Africa back to 3–3.5 Mya, with the probability in favour of the earlier figure. Again, while showing undoubted bipedal adaptations, especially in the rear of the foot, the indications of a widely divergent and mobile big toe are consistent with significant arboreality (Clarke and Tobias, 1995).

The species *A. afarensis* and *A. africanus* are differentiated primarily upon contrasts in dental proportions and associated facial and masticatory features. Postcranial contrasts, although much discussed, were long thought essentially trivial, as McHenry (1986) emphasized. However, recent postcranial discoveries at Sterkfontein, in particular a partial skeleton Stw 431, point to intriguing locomotor contrasts as well (McHenry and Berger, 1998). *A. africanus* has larger, more powerfully muscled forelimbs and smaller hindlimbs compared with *A. afarensis* (and, less certainly, *A. anamensis*), which were more similar to modern humans in relative limb proportions. The *A. africanus* material, on the other hand, resembles *Homo habilis* specimens in its proportions (see below). It is very likely that some of the differences in facial structure, tooth size and shape, minor postcranial details, etc., occurred initially as sampling accidents and subsequently became enhanced and fixed through reinforcing selective forces. However, contrasts in dental wear indicate differing selection pressures associated with food processing requirements in the two regions (see below).

Between 2.2 and 2.6 Mya East African sites in the Omo valley and at West Turkana yield the first evidence of 'robust' australopithecines. The earliest species is *A. aethiopicus*, best known from the 'Black Skull' (WT 17000) dated at *c.* 2.6 Mya. This is a relatively small-brained (400 cm³), massively built specimen with large sagittal crest, strong supraorbital torus, massive cheek teeth and large anterior dentition set in a markedly prognathous face.

Later East African specimens assigned to *A. boisei* (2.0–1.4 Mya) are bigger brained ($500+ \text{ cm}^3$) and, while possessing massive cheek teeth, show much reduced incisors and canines set in a flatter, deeper mid- and lower face. The cheek region extends further forward than in *aethiopicus*, and the sagittal crest is smaller, in part a consequence of the expanded brain case, but also reflecting the more vertically directed temporal muscle.

Similar, although less extreme, features are seen in the South African robusts from Kromdraai and Swartkrans. While traditionally included within the single species *A. robustus*, in recent years there has been a tendency to differentiate specimens from the two sites by following Broom's original specific distinction. The Kromdraai specimen (*A. robustus*) is rather more lightly built and has smaller cheek teeth than the Swartkrans sample (*A. crassidens*).

There are undoubted similarities between the South and East African robusts, but contrary to some earlier views expressed (including mine), detailed differences in facial anatomy, cheek morphology and dental proportions indicate that they were specifically distinct. However, *A. robustus* and *A. boisei* are clearly the same sort of animal with similar features: expanded cheek teeth (megadonty); broader, deeper, more orthognathous face with reinforced mid-facial region; lower, flatter cranial vault and flexed basicranium; and anteriorly situated zygomatic region with large masseter muscle and main masticatory force directed over the molar region. Postcranial morphology and proportions are, so far as we know, similar in the two species but with some terrestrial refinements compared with *afarensis* and *africanus*. For all these reasons a growing movement has favoured resurrecting Broom's genus *Paranthropus* for these fossils, to distinguish them from the earlier *Australopithecus* and to reflect their inferred monophyly (derivation from a single ancestor) and common adaptive base (but see below).

These later robusts date from around 2 Mya, or slightly earlier, down to about 1.4 Mya (or possibly down to *c.* 1 Mya in the case of Swartkrans). From just under 2 Mya the range of hominid diversity is further extended by other forms, usually assigned to the genus *Homo*. The longest known is *H. habilis*, best known from Olduvai and around Lake Turkana, but also represented in the Omo Basin and South Africa in Sterkfontein Member 5. *Habilis* appears to be a small-bodied, moderately brained ($500\text{--}770 \text{ cm}^3$) hominid with progressive teeth and jaws but, on the basis of two partial skeletons (OH 62 and KNM ER 3735) a remarkably primitive postcranial skeleton. Hindlimbs were short and lightly built, forelimbs long and powerfully muscled, suggesting arboreal activity, while the

labyrinth of the inner ear, revealed in the Stw 53 cranium, is unlike that of modern humans or apes (Spoor et al., 1994). In fact *H. habilis* is probably best thought of as a late (?relict) australopithecine species that represents something near the tail end of the Mid-Pliocene hominid radiation, and whose dental and neurocranial features were probably acquired independently of other early *Homo*. Brain expansion certainly seems to have characterized more than one hominid lineage: later robusts show something like a 25 per cent increase in cranial capacity compared with WT 17000.

A second, essentially contemporaneous, species is *Homo rudolfensis*, known only from the Koobi Fora sites east of Lake Turkana dated between 1.7–1.9 Mya, and based on specimens such as KNM ER 1470, 1590 and 3732. This was bigger brained than *habilis* (770–850 cm³) with a broader, flatter face and larger, more complex cheek teeth. The 1470 skull – the best preserved specimen – shows cranio-facial features that in some respects mimic robust australopithecines, whilst also possessing traits that reveal its distinctiveness from the robusts. The face is broad, deep and flat, with deep, anteriorly situated and antero-inferiorly sloping maxillary zygomatic processes, but neurocranial form is different from any australopithecine, and the cheek teeth, while large-crowned and with a complex root system, are non-robust. Its phyletic status remains enigmatic pending the recovery of more cranial material (is 1470 atypical?) and, above all, associated cranial and postcranial remains. These are currently lacking, but the cranial dimensions suggest a bigger body size than most *habilis* individuals, and there are appropriately sized isolated postcrania from the relevant Koobi Fora deposits (1.9 Mya), including femora (e.g. ER 1481) and a hip bone (ER 3228) of rugged but broadly modern morphology.

Alternatively, these may represent the earliest evidence of a third human species, early *H. erectus* or *H. ergaster* (see below; in the meantime hereafter referred to as *H. erectus*). The oldest definite (i.e. cranial) evidence for this is the well preserved ER 3733 cranium dated to 1.78 Mya, followed by the rather younger and less complete 3883 cranium and the remarkably preserved WT 15000 skeleton, both around 1.5–1.6 Mya. The isolated postcrania referred to above are closely matched in the 'Turkana boy' skeleton, increasing the probability that they represent evidence for *H. erectus* predating the defining cranial remains. In this case they would push the species' origin back to around the 2 Mya boundary or even before, in which case the origin and affinities of both *H. erectus* and *H. rudolfensis* remain obscure (see below).

Similar obscurity surrounds the fragmentary SK 847 specimen from Swartkrans which, while undoubtedly *Homo*, has been claimed

as both *H. habilis* and *H. erectus*. However, Bilborough and Wood (1988) noted differences from both these species, as did Grine et al. (1993 and 1996). Grine et al. conclude that the specimen may well represent yet another species of early *Homo*, currently unknown (or at least unrecognized) in East Africa.

The earlier evidence: overview and assessment

The increasing number of species evident in the African Plio-Pleistocene fossil record points to a radiating array of early hominids, and enhances the probability of contingent events influencing individual clades. Moreover, the relevant palaeoenvironmental evidence reinforces the picture of chance factors affecting particular populations. In East Africa broader climatic fluctuations combined with regional changes resulting from altered drainage patterns due to tectonic instability and periodic ash falls blocking river systems, with profound effects on the local faunas and floras. The phenomenon is best documented in the Turkana basin, but undoubtedly occurred elsewhere.

Tectonic activity was not a feature of the South African highveld, but other variables are likely to have had comparable and similarly dramatic effects. In such seasonal environments minimal (i.e. 'normal') short-term climatic fluctuations, especially of rainfall, when combined with the porosity of the limestone substrate, can be expected to have had reinforcing, pendulum-like impacts on the locally differentiated plant and animal communities. The complete disappearance of free-standing water from streams and water holes must have been a frequent if unpredictable occurrence in some australopithecine habitats, with resulting local extinctions. There are other pointers as well: the marked dental attrition, amounting to virtual destruction of the entire tooth crowns of mature South African specimens, and not seen in East African hominids, indicates strong selection for a powerful masticatory apparatus and resistant dentition (thick enamel, etc.). This in turn reflects the marked seasonality and ensuing bottlenecks of food availability referred to above. It has been argued that towards the end of the dry season only hard-cased nuts, fruit and berries, and underground items such as bulbs, tubers and rhizomes would have withstood desiccation and so been available as potential food items. Such a regime would have placed a premium on both behavioural flexibility and masticatory power.

The common features of robusts, especially their cranio-dental characteristics, have usually been interpreted as strong evidence of monophyly (see, for example, Wood, 1988; Grine, 1988; Skelton

and McHenry, 1992; Strait et al., 1997), but there are also strong morphological continuities between *A. africanus* and *A. robustus* in South Africa, with the former foreshadowing the latter, and between *A. aethiopicus* and *A. boisei* in East Africa. It is not possible to accommodate this pattern of affinities in any single phyletic scheme without a degree of parallelism, whether between *africanus* and *robustus/boisei* if the latter are monophyletically derived from *aethiopicus*, between *robustus* and *boisei* if these are independent developments in the two regions, or between *aethiopicus* and *robustus/boisei* if the latter are monophyletically derived from *africanus*, as preferred by Skelton and McHenry (but see Strait et al., 1997). The evolution of robust cranio-dental form may have been inevitable, given mid-Pliocene hominids' response to shifting environments and selection pressures after about 2.5 Mya, but the morphological details were doubtless contingent upon pre-existing anatomical patterns, themselves the products of, and further mediated by, the vagaries of sampling fluctuations on small populations.

If this interpretation is correct, contrasts in facial architecture as documented by Rak (1983) probably do not reflect a phyletic sequence as originally argued, but rather different ways of achieving the same functional goal – greater occlusal (chewing) power – from different origins, with the detailed outcomes contingent on the starting points i.e. the antecedent species, and subsequent multiple bottlenecking episodes in the two regions.

Other aspects of robust evolution are discussed by Foley (Chapter 3): relatively frequent in the fossil record between 1.5 and 2.3 Mya, robust numbers decline thereafter. The latest *A. boisei* specimens are c. 1.2–1.4 Mya, while *A. robustus* may last down to c. 1.0 Mya in Member 3 at Swartkrans. Klein (1988) suggests that the major climatic and environmental switch at c. 0.9 Mya may have delivered the coup de grace to the robusts, but evidence points to dwindling numbers well before that date. Their disappearance may well be associated with the general faunal turnover that occurred c. 1.5–1.3 Mya, when generic numbers were reduced significantly, reflecting the decline and extinction of Pliocene forms, and their replacement by more modern taxa. Irrespective of the underlying causes, as numbers declined chance factors can be expected to have assumed an increasingly prominent role in the survival or extinction of local communities and eventually of entire species.

Whatever the resolution of these issues, the evidence clearly points to an array of early *Homo* forms comparable to, and presumably derived from within, the early–mid Pliocene hominid radiation. Their mosaic affinities – one to another and with other

hominids such as the robust australopithecines – their environmental associations and regional distributions, with their resulting parallelisms, are all compatible with interpretations that plausibly view them as outcomes of habitat fragmentation consequent upon the drier, more seasonal conditions of the later Pliocene. Stochastic factors are thus likely to have been significant and influential in such circumstances, and contingency deeply implicated in the origins of our own genus, as well as in the disappearance of *Australopithecus*.

The terminal Pliocene thus represents a period of unparalleled hominid diversity, but there is a marked contraction around, or shortly after, the Pleistocene boundary. *H. rudolfensis* is unknown after about 1.7 Mya, *H. habilis* after about 1.5 Mya. *A. boisei* and *A. robustus* may linger on for some time thereafter (see above), but their numbers decline sharply in the fossil record. *H. erectus* remains, on the other hand, turn up with increasing frequency in the basal Pleistocene of East Africa and then elsewhere.

Homo erectus and Homo ergaster

The origins of *H. erectus* are unknown, but the Turkana record dates it certainly to at least > 1.8 Mya, and probably to > 2 Mya if the individual postcrania discussed above are correctly referred to that taxon. It is also clear from the discoveries around Lake Turkana that the species represents a distinctive, functionally-integrated anatomy (morphotype) and an abrupt break with earlier hominid morphologies. The cranio-dental features (small teeth and reduced molars, lightly constructed face and jaws, short, broad, palate and expanded neurocranium but with large supraorbital torus, thick vault bones, large, sharply angled occipital with prominent nuchal area and distinct torus) are distinctive in combination, and contrast with those of other early hominids.

Postcranial contrasts, as revealed by study of the WT 15000 skeleton (Walker and Leakey, 1993), are even more striking. This shows strongly muscled and ruggedly built but essentially modern trunk and limb proportions that have been plausibly interpreted as adaptations to a terrestrial niche in hot, dry, open (i.e. savanna) environments in contrast to the more wooded, closed contexts of earlier hominids (and, to judge from the postcrania, of *H. habilis*). There are no obvious antecedents for this morphology, but again, the widespread evidence of drier, more seasonal environments after c. 2.5 Mya was presumably a major driving force in its evolution.

In this respect the lack of definitely associated postcranial remains of *H. rudolfensis* is particularly vexing. If the ER 1481 femur, 3228 hip bone, etc., belong with the ER 1470, 1590, 3732 crania rather than

the 3733/3883 group, they suggest that *H. rudolfensis* and *H. erectus* were effectively indistinguishable below the neck, so implying close phyletic relationship and a recent common ancestor. However, such a conclusion is difficult to reconcile with the extensive cranio-dental contrasts, and in fact the pattern of affinities based on characters of the skull and dentition suggests closer links between *H. erectus* and *H. habilis*, despite their markedly contrasting postcrania (Lieberman et al., 1996). More well-provenanced material is necessary to resolve this conundrum, but a substantial degree of parallel evolution appears to typify basal *Homo*, as other early hominids.

Whether the earliest African representatives of *erectus* morphology are sufficiently distinctive from the later, predominantly Asian specimens that comprise the species type-sample (hypodigm) to warrant species differentiation remains a moot point. Some cladistic studies of the relevant material over the last decade or more (e.g. Wood, 1984; Andrews, 1984) have advocated separation, and Wood (1991, 1992) has adduced further detailed argument for recognizing the Koobi Fora specimens as a more primitive species, *H. ergaster*. While the case has been accepted by some (e.g. Howell, 1994; Tattersall, 1995; Foley, 1995), such studies and their conclusions have been criticized by others (e.g. Turner and Chamberlain, 1989; Bilsborough, 1992; Brauer and Mbau, 1992; Harrison, 1994) for failing to take adequate account of the internal variability of the African and Asian samples, vitiating the claimed autapomorphies (uniquely-derived features), and so the case for specific distinctiveness itself.

Should further evidence or detailed study resolve the issue in favour of the distinctiveness of *H. ergaster*, then the very evolution of *H. erectus* as a hominid species occupying (adapted to?) a predominantly Asiatic zone might be cited as an example of contingency in hominid evolution. Even so, difficulties remain. Walker and Leakey (1993) make clear their preference for *erectus* rather than *ergaster* for the Nariokotome specimen, and there is general agreement that the somewhat younger (1.2 Mya) Olduvai OH 9 specimen represents, on even the narrowest definition, *H. erectus*, not *ergaster*.

In other words, the case for *H. ergaster*, and a predominantly Asian habitus for *H. erectus*, remains non-proven at best, and I therefore incorporate both African and Asian specimens within *H. erectus*, i.e. as conspecific. In fact, this debate over the affinities of early African *erectus* provides a prime example of the extent to which conceptual frameworks and methods employed can influence phyletic conclusions (Bilsborough and Wood, 1986; Walker, 1993).

Morphological stability and geographical expansion, both within

Africa and beyond, show *H. erectus* to have been a highly successful species. While there is evidence for chronological change in cranio-dental features (brain expansion, vault proportions, tooth reduction etc.), postcranial characters remain remarkably constant, with specimens well over one million years younger than WT 15000 showing similar features (Ruff, 1995). Such postcranial diversity as occurs is plausibly interpreted as polytypism (continuous intra-species variation), e.g. the shorter stature of the high-latitude Zhoukoudian sample may reflect climatic adaptation (Allen's 'Rule') or impaired growth due to nutritional stress in markedly seasonal conditions.

Early expansion beyond Africa

It has been customary to view hominid expansion out of Africa as a relatively late and extended phenomenon, initiated some time before one million years ago, but with hominids absent from large areas of Eurasia until around the Lower/Middle Pleistocene boundary, or even later. However several recent discoveries challenge that interpretation and point to the possibility of considerably earlier, even *pre-erectus*, migration. In my view the evidence is far from secure and I remain sceptical of such early colonization, but, if eventually confirmed, it looks set to refashion our frameworks for human occupancy of Asia and Europe in much the same way as the first potassium argon dates from Olduvai did for African prehistory. In this context the main point is that early migration and extended occupancy of variable higher latitude environments by socio-culturally and technologically primitive hominids would greatly increase the importance of contingent influences in human evolution.

Probably the most secure early extra-African hominid occurrence is that at 'Ubeidiya, Israel (and so relatively proximate to the presumed origin) dated to c. 1.3–1.4 Mya. Here there is extensive archaeological evidence (Developed Oldowan and early Acheulean) and fragmentary remains of *Homo*, insufficient for specific identification (Tobias, 1966). A more recent discovery is the virtually complete mandible body and dentition from Dmanisi, East Georgia, more or less midway between the Black and Caspian Seas (Gabunia and Vekua, 1995). This is associated with a Late Villafranchian fauna and Oldowan-like tools above a basalt dated to 1.8 ± 0.1 Mya; both basalt and faunal level have normal polarity, and are therefore assigned to the Olduvai event (> 1.77 Mya). The specimen has accordingly been widely regarded as evidence for early *Homo* at the 'gates of Europe' around the Plio-Pleistocene boundary.

However, there are difficulties. The finds were recovered during excavations of a mediaeval town, with grain storage pits beneath the houses. The mandible is from one such pit, with obvious potential for a mixed deposit, and may therefore not be contemporary with the fauna, while uncertainties have been voiced about the geomagnetic polarity (Dean and Delson, 1995). The mandible's affinities are clearly with *H. erectus* rather than other early *Homo* (Gabunia and Vekua, 1995; Dean and Delson, 1995) and, moreover, later *erectus* at that (Brauer, 1995), which raises the possibility that the normal polarity, if not an artefact, indicates a Brunhes age (< 0.78 Mya). Until these uncertainties are resolved it seems premature to recast the chronology for human occupation of Eurasia.

Much the same applies to early dates from East and South East Asia. Swisher et al. (1994) have published $\text{Ar}^{40}/\text{Ar}^{39}$ dates of 1.81 ± 0.04 Mya and 1.66 ± 0.04 Mya for the Modjokerto (Perning) and Sangiran hominid sites in Java, but these have been criticized as conflicting with biostratigraphic, palaeomagnetic and fission track profiles from the area, and for their dissociation from the hominid specimens (de Vos and Sondaar, 1994; see also Swisher, 1994). The bulk of the evidence suggests that the earliest Javan hominids are around 1.2 My old (see below).

Possibly the earliest instance of *Homo* on the Asian mainland is that from Longgupo Cave, Sichuan Province, central China (Huang et al., 1995). Here a hominid left mandible fragment with second premolar and first molar, and a right upper lateral incisor were recovered from a clay channel in levels 7 and 8 of the cave infill's middle zone (the levels are not stratigraphically defined, but correspond to 1 m spits). Also recovered from the 11 metre-thick fossiliferous middle zone were two possible artefacts and an extensive fauna, including monkeys and *Gigantopithecus*. The assemblage appears to be the result of carnivore and scavenger action (possibly combined with accidental falls), subsequently transported by water action within the cave system. Overall the fauna suggests a late Pliocene/basal Pleistocene age.

A palaeomagnetic column for the upper and middle zones consists of seven magnetic reversals, with normal sediments thinner than reversed sections. Huang et al. cannot completely exclude the possibility of selective remagnetization and so a false profile, but consider it unlikely. Because of the fauna, the authors assign the magnetically normal hominid levels 7 and 8 to the Olduvai event (1.78–1.96 Mya). ESR dating of a cervid tooth from level 4 gives dates of 0.75 ± 0.09 Mya assuming early uptake, and 1.02 ± 0.12 Mya on linear uptake. The authors prefer the latter as consistent

with the palaeomagnetic evidence in indicating a Matuyama age for level 4, and Olduvai event age for levels 7 and 8.

The surprisingly early date for the hominid material depends essentially upon the identification of the fauna as late Pliocene/basal Pleistocene; of themselves the palaeomagnetic column and ESR dates are consistent with a later Matuyama age, with the normal polarity of levels 7 and 8 perhaps reflecting the Cobb Mountain (1.14–1.2 Mya) or Jaramillo (0.9–1.02 Mya) events. It is therefore frustrating that few details are available about the relationship of the hominid remains to the other faunal elements, and whether the latter show significant change, as might be expected over the apparently long interval represented by the middle zone deposits.

The hominid jaw fragment and teeth differ from later Asian *H. erectus* in size, shape and occlusal morphology, and resemble early East African specimens assigned to *H. erectus* (*ergaster*) or *H. habilis*. The authors refer the specimens to *Homo* sp. indet. while making clear their view that they represent a more primitive, antecedent species to Asian *H. erectus*. The fossils' characteristics are consistent with a basal Pleistocene date but this is not in itself conclusive, since they are equally consistent with a later Lower Pleistocene age. On the other hand, the contrasting affinities of the Dmanisi and Longgupo mandibles are noteworthy, making it difficult to view them as representatives of a single expansion from Africa, which the claimed dates *prima facie* suggest.

The Longgupo artefacts (a spherical cobble 'pounder' and lenticular flake with multiple scars) are foreign to the locality, twice the size of the largest normal clasts and show damage suggestive of use; they are of broadly 'Oldowan' type. The difficulties in recognizing such tools, especially out of primary context (Roebroeks and van Kolfschoten, 1994), suggest caution before concluding that they are definite artefacts. Overall, the Longgupo Cave finds point to Lower, but not necessarily basal, Pleistocene hominids in East Asia, consistent with other mainland and South East Asian evidence (see below).

Continental and South East Asia

Despite the recent focus on African finds, the Javanese fossils still comprise the largest cranial sample of *H. erectus*, as well as the original type-specimen (holotype). As representatives of small populations, intermittently isolated as a result of fluctuating sea levels and at the extreme periphery of Lower-Middle Pleistocene human distribution, in principle they provide an ideal test bed for

the identification of plausible contingencies in human evolution. Founder effects, genetic drift, localized selection pressures and chance events, when combined with small population numbers, might all be expected to have been major influences on local morphology. They might also be considered to be significant promoters of speciation, with differentiation of Javan *H. erectus* from the populations of mainland Asia and elsewhere and, indeed, possible differentiation within Indonesia itself. How does the evidence measure up to this interpretation?

There is reasonable evidence within the Javanese sample for some local differentiation and continuity, with certain cranial features displaying heightened frequencies. They include: a pronounced supraorbital torus that shelves directly into the frontal with little or no supratatorial sulcus, frontal and parietal sagittal keeling with associated parasagittal depressions, prominent angular torus, and a flattened, plate-like nuchal region delimited by a distinct torus. However, while these features are common within the Javan specimens, they are neither ubiquitous nor exclusive to the sample. And against the claims for regional differentiation has to be set the evidence for continuity with mainland Asian fossils. The similarities between Javan and Chinese *erectus* fossils are so marked that most workers view them as sub-specifically distinct at best.

Claims for specific distinctiveness within Java, or between Java and the mainland, fall into three broad categories:

1. excessive taxonomic splitting ('discoverer's bias') without justification, which characterizes some accounts of the Javan fossils.
2. claims for the presence on Java of other hominid species besides *H. erectus*. These are invariably based on extremely fragmentary material (usually limited jaw and dental remains) and on features with known interspecific overlap between early hominids, while ignoring contrasts that undoubtedly exist in other features. Examples include claims for robust australopithecines based upon mandibular corpus robusticity while ignoring contrasts in associated premolar and molar teeth; claims for *H. habilis* based on similarities in dental size and proportions between Javanese and Olduvai specimens, ignoring the undoubted contrasts in neurocranial size, proportions and robusticity.
3. as noted above, claims based on comparisons with the relevant East African fossils, for the specific distinctiveness of Asian *H. erectus*. A recent example is Howell (1994) who effectively combines (2) and (3), arguing for multiple taxa among the Javan

fossils while making clear his view that all are referable to *Homo*. He suggests that *H. habilis* and/or *H. rudolfensis* may be represented in the dental and gnathic samples (e.g. the 'Meganthropus' fragments), but others contest this view, and the Javan neurocranial remains, in particular, are all strikingly similar.

Rather, what impresses with the Javanese material is its homogeneity, not only internally but in relation to other specimens from mainland Asia. Earlier Chinese specimens such as Lantian are comparable to the Sangiran 4 and 17 crania (the latter is the only Javanese fossil to preserve the face) while later material such as ZKD 5 (China) and Sambungmachen (Java) shows a degree of cranial expansion, a heightened vault, similar morphology of the supraorbital region, and comparable reduction in temporal and nuchal reinforcement of the vault. These phenomena presumably reflect either parallel evolution of similar features in response to comparable selection pressures on mainland Asia and Java, or successive colonizations of the latter by earlier and later continental *erectus*. What they do not point to is any support for specific distinction between Middle Pleistocene mainland and Sundaland hominids and, so far as I am aware, no convincing demonstration of this has been provided.

In fact, the best example of possible regional differentiation is provided by the comparatively late (final Middle or earliest Upper Pleistocene) Ngandong (Solo) sample. In many respects these crania display further development of the features noted in ZKD 5 and Sambungmachen: neurocranial expansion, diminution of nuchal and masticatory reinforcement, etc. However, this later pattern is not currently known from continental Asia, and is best thought of as a 'terminal, presumably insularly derived product of the *H. erectus* clade' (Howell, 1994). Howell summarizes the material's biostratigraphic associations, pointing out that virtually all taxa are continuations of earlier immigrant species, providing no evidence for continental connections at the time of the Ngandong population. However, while advocating multiple species recognition among Asian hominids, Howell, like all other workers known to me, differentiates the Ngandong material only sub-specifically as *H. erectus soloensis*. A convincing example of hominid regional differentiation thus remains a micro- rather than macro-evolutionary phenomenon. It also points to a degree of directional (anagenetic) change, rather than random short-term oscillations as predicted by rigid application of the punctuational model to the Javanese hominids.

By this time (later Middle/basal Upper Pleistocene) other, more progressive morphologies are represented at mainland sites such as Yunxian, Dali, Dingcun, and Xujiayao in the centre and north of China, and Maba in the south. The specimens are described by Pope (1991, 1992) and Howell (1994), who also consider their contextual and stratigraphic associations. While Pope focuses on commonalities and the distinctiveness of Asian compared with non-Asian fossils, Howell emphasizes the diversity of this material and severely criticizes the usual referral to archaic *H. sapiens*. In particular, he distinguishes between a southern morphology as represented by Maba, which he links with the Narmada (Madhya Pradesh, India) cranium, and the other Chinese fossils from higher latitudes, which of themselves constitute a pretty variable sample.

Disentangling the affinities of these specimens awaits detailed comparative treatment, but the main point here is their disjunction from *erectus* morphology. They presumably represent either immigrant populations into East Asia from further west, replacing *H. erectus*, or local descendants of that species. Chinese workers and others (e.g. Wolpoff, Wu and Thorne, 1984; Pope, 1991, 1992; Wolpoff et al., 1994) have stressed cranio-dental traits that point to a degree of continuity between continental *erectus* and this material, so that the latter interpretation seems the more plausible. The absence of intermediates and the late dates of the uppermost Zhoukoudian (0.26 Mya) and Hexian (<0.2 Mya) *erectus* (Pope, 1992) suggest origin by speciation rather than anagenesis although recent work suggests the upper ZKD levels may be >0.4 Mya, and the lower deposits of terminal Lower Pleistocene age.

More detailed studies are sorely needed, but the later Asian fossils therefore provisionally suggest contrasting evolutionary patterns in East and South East Asia: in the former region abrupt change probably associated with speciation event(s), in the latter less marked (though still significant) change and stronger evidence of continuity, together suggestive of anagenesis. On biogeographical grounds this seems the wrong way round to what might be expected of continental and insular faunas, but the climatic fluctuations of the later Middle Pleistocene were more marked and doubtless more disruptive in higher latitudes than in the Malaysian region. Indeed, climatic change is likely to have been a major determinant of the East Asian record in the north, whether by promoting speciation as suggested above, or replacement by migration and re-colonization.

In any event, the similarities noted between East and South East Asian hominids extend over much the greater part of the period since human occupation of the continent. On the standard (short)

chronology this would be perhaps 0.8–1.0 My (<1.2 Mya–0.1 Mya). If the recently announced Longgupo and Sangiran dates are correct, the chronology is extended to 1.5–1.7 Mya. For the reasons noted above, such a time-frame is, in my view, unlikely (and certainly far from proven) but its extension would make the morphological similarities between the mainland and Indonesia even more remarkable.

Europe

There are hints, both archaeological and fossil, of early (i.e. pre-Middle Pleistocene) hominids in Europe. Possible artefact sites include Vallonet and Soleilhac, but their claims for hominid origin and antiquity are both fragile. Isernia, another more securely hominid and supposedly early tool site, has recently been redated from >0.73 Mya to <0.5 Mya. Hominid fossil evidence is possibly provided by the sites of Venta Micena, Barranco Leon and Cueva Victoria around Orce in south east Spain (Gibert, 1995), and more definitely by Gran Dolina (TD 6), Atapuerca, in the north west of that country (Carbonell et al., 1995). This last site has yielded dental remains and cranial, mandibular, and postcranial fragments of at least four individuals, together with broadly Oldowan-like cores and flakes from an horizon with late Biharian micro-fauna and reversed polarity, indicating an age of >0.78 Mya. A well-preserved frontal shows minimum breadth considerably greater than most African and Asian *H. erectus*, and also contrasts with these in its double arched, rather than horizontal, supraorbital torus. This, some dental and especially mandibular traits all show continuity with later European hominids, including those from the Middle Pleistocene Sima de los Huesos, also at Atapuerca (see below).

While Gran Dolina represents the most convincing evidence for a Lower Pleistocene hominid presence in Europe, the bulk of the evidence is relatively abbreviated, with a maximum age of 0.5 Mya or thereabouts (Heidelberg and Boxgrove), and the great majority of specimens much younger. This in turn suggests a comparatively late occupation – or at least a late *extended* occupation – of the continent, as opposed to possible earlier transient forays or a precarious toehold on its extreme southern margin. Gamble (1993) and Roebroeks and van Kolfschoten (1994) review the arguments and evidence for a short European chronology. Turner (1992) has suggested that changing faunal patterns, especially of larger carnivores such as sabre-toothed and dirk-toothed cats, and scavengers (giant hyenas) made entry into much of Europe particularly difficult for hominids between 1 and 0.5 Mya. An

exception would be Iberia, which lacks the giant hyenas that Turner views as direct scavenging competitors of early hominids, and it is noteworthy that that region has subsequently provided the most secure evidence of early humans.

Again it is easy to envisage random factors significantly influencing early European human evolution, given their small population numbers and isolation following from the peripheral location, varied topography and fragmented habitats, and of course, the effects of the multiple climatic oscillations of the last million years. Indeed, Gran Dolina suggests that some regional features characterizing European hominids, and which persist for the greater part of the later Quaternary, were established very early in the sequence, perhaps reflecting founder effect.

Prior to about 100,000 years ago postcranial evidence is extremely limited, and what there is shows few, if any, contrasts with *H. erectus* postcrania up to 1.5 My earlier. Cranial remains are more numerous, and have traditionally been assigned to archaic *H. sapiens* as *H. s. steinheimensis* or *H. s. heidelbergensis*. However, Tattersall (1986, 1992, 1995) has argued, rightly in my view, that this material should be accorded specific status, and he proposes *H. heidelbergensis*. Interestingly his species *heidelbergensis* is not confined to Europe, but also includes material from sub-Saharan Africa such as Bodo and Kabwe. If correct, it suggests a fair morphological range for at least this particular Middle Pleistocene human species. Alternatively, *H. heidelbergensis* should be restricted to the European material, with the African specimens distinguished as a separate species, perhaps *H. rhodesiensis*.

Many European cranial specimens show distinctive features such as a suprainiac fossa, occipital bunning, anteriorly projecting mid-face with salient nasal bones and inflated malar region, long mandibular corpus with retro-molar space, and a continuous supraorbital torus, that is semicircular above each orbit. The earlier fossils (> 0.2 Mya) usually display just one or two of these features, but after about 0.12 Mya they turn up repeatedly in combination in (usually) bigger brained specimens displaying a typically elongated cranial vault morphology, and associated with distinctive postcranial anatomy, so forming part of the characteristic Neanderthal morphology.

Neanderthal remains extend across Europe eastwards into the Russian Federation and southwards into the Middle East and south central Asia. As is well known, in the Middle East, dates suggest considerable temporal overlap between Neanderthals (Tabun, Shanidar, Kebara) and individuals with broadly modern anatomy (Skhul, Qafzeh) between 100 and 60 kya, suggesting movement of

human groups from north and south into the area as a 'frontier zone'. In Western Europe the record indicates an abrupt switch in morphology around 35–30 kya, pointing to the intrusion of modern anatomy into the region, and replacement of Neanderthals rather than *in situ* evolution.

The peripheral distribution of Neanderthals and their association with periglacial conditions as well as their morphology, have led many workers to view them as a distinct subspecies or species, differentiated as a result of isolation in higher latitudes and adapted to cold environments. Body form and limb proportions certainly accord with what might be expected in such climates, but it is difficult to view many Neanderthal features, including all those listed above, in this way. Nor is it at all easy to interpret all Neanderthal characters as contributing in any consistent and obvious way to a tightly integrated functional morphology, (although the persistence of that morphology over at least 70–80 ky implies that it was not ineffective or maladaptive). In other words, an adaptationist analysis cannot adequately account for all features that regularly form part of the Neanderthal morphotype.

Some earlier fossils throw additional light on this problem. Most of the European Middle and early Upper Pleistocene evidence consists of individual – and usually incomplete – specimens. However, the extensive sample (700 fossils, representing at least 24 individuals) from the Sima dos Huesos, Atapuerca (Arsuaga et al., 1993) includes several recently recovered and relatively complete crania and mandibles dated to >0.3 Mya. They are remarkably variable, with some specimens displaying just a few of the features noted above (such as supraorbital torus and occipital morphology) upon a generalized robust Middle Pleistocene cranium, while others exhibit a more extended set of Neanderthal features. Evidence points to the specimens representing a single local population which, if typical of other such communities, indicates marked internal diversity in European Middle Pleistocene human groups. At some point, probably a cold phase in the late Middle Pleistocene, a bottleneck effect produced by reduced population numbers led to a reduction in diversity and the fixation of Neanderthal features in these European groups.

If the origin of Neanderthals resides in contingent events, so too probably does their disappearance. To judge from the archaeological record, the earliest *H. sapiens* in sub-Saharan Africa and the Middle East are indistinguishable in behaviour, technology and subsistence from their regional contemporaries of more archaic morphology. As is well known, the much later European record does indicate differences, but even here their initial magnitude has,

in my view, been overstated. Many of the Upper Palaeolithic innovations stressed in such contrasts do not characterize the very earliest Aurignacian horizons, but come in rather later (and then, incidentally, disappear again for considerable periods). Moreover, if, as the St Cesaire fossil indicates, the Chatelperronian lithic industry was an indigenous Neanderthal response to new techniques and tool kits filtering westwards, it points to an impressive capacity for change, flexibility and assimilation that in turn suggests a high degree of adaptability and learning capacity. The oft-asserted superior cognitive ability of *Homo sapiens* seems to me to be wide of the mark.

Of course, there has to be some underlying explanation(s) for the expansion of *H. sapiens* and the disappearance of Neanderthals and other archaic forms. For me the most plausible interpretations focus on some currently ill-defined socio-cultural or technological differences between the groups. These conferred a slight but real and self-reinforcing (autocatalytic) demographic advantage on (some) *H. sapiens* groups; Zubrow (1989) has shown how such a differential could lead to the rapid (within a thousand years) extinction of the less favoured group. In Europe this happened to be the Neanderthals, but it could just as well have been the other way around, if they had happened to innovate socio-culturally at the appropriate time. My point is that there is no necessary link with modern morphology, no compelling case for superior cognitive ability on the part of *H. sapiens*, and that the inferred innovations do not coincide with the origination of the species as defined morphologically. Nor need we assume – as is usually the case – that all *sapiens* groups were invariably successful in their interactions with others. Some doubtless failed, just as they have in historic times, both in competition with archaics and against other *sapiens*.

It is also possible that the disappearance of European Neanderthals had little or nothing to do with the appearance of anatomically modern humans in Central and Western Europe. We tend to compress Neanderthals into a relatively short time-frame when, in fact, they covered a considerable period, and at any given time population numbers could have been very low. A bottleneck effect, by definition, implies reduced numbers, and the population may well not have recovered to its former size, but instead dwindled over an extended period to the point of no return. On this interpretation the juxtaposition of late Neanderthals and early moderns would be fortuitous, not causally related, except in the sense that Neanderthal decline freed space and resources for modern immigrants into Europe.

If correct, this would provide a prime example of contingency in the early evolution and radiation of our own species. However, as an explanation it should be seen as complementary to the socio-cultural advantage referred to above, not an alternative, since it cannot itself account for the disappearance of *all* archaic morphologies (non-Neanderthal as well as Neanderthal) – unless, that is, we invoke pan-catastrophism.

Modern human origins

Just as it is impossible to account convincingly for all Neanderthal features in functional or adaptive terms, so too with modern morphology. While the general linearity and gracility of the trunk and limbs can plausibly be related to thermoregulation in hot environments, the adaptive basis of certain cranial features is more problematic. It is comparatively easy to envisage the selective value of a large face and powerful jaws, but what benefits accrue from possessing a flat face, weak, crowded jaws that predispose to malocclusion and potentially fatal dental pathologies, and a thin, globular braincase? The ubiquity of such features makes it impossible to tie them into specific environments, and it is difficult to see what general advantage might derive from small, light structures sufficient to explain the rapid, universal and sustained reduction in facial size of the Upper Pleistocene. Relaxed selection for larger faces is of itself inadequate to account for the diminution, and so many workers have agreed with Smith (1983) that once a larger face is no longer needed the energetic cost of maintaining it means that smaller faced individuals will have a selective advantage. However, this 'general economy' argument is also hardly a convincing explanation for the scale and pace of change, and the disappearance of large-faced forms.

Given the complexity of the (largely unknown) genetic and developmental factors underlying skeletal variation, two other interpretations warrant consideration. The first is that many of the archaic-modern contrasts are due to pleiotropic gene effects (i.e. genes having multiple influences on form), that are selected for because of a minority (by no means necessarily the most obvious or marked) of those influences. Neutral, near neutral, and even mildly disadvantageous characters may be dragged along for the evolutionary ride if they share a common morphogenetic base with other features strongly promoted by selection. If correct, many of the defining features of our own species may be functional irrelevancies, hallmarks of *Homo sapiens* only through genetic association.

It is also very likely that there is a significant component of phenotypic lability involved in many of the contrasts either side of the archaic-modern transition. Environmental factors – e.g. biomechanical forces – are known to exert significant influence on skeletal form, particularly during growth and development, so that rapid and marked morphological contrasts do not necessarily imply equivalent evolutionary (genetic) change. Phenotypic responses of this kind are apparent in the reduced face and jaws associated with the shift from hunter-gathering to agriculture (see Larson, 1995 for a recent review), and there is no reason to exclude them from contributing to earlier changes.

As is well known, the issue of modern human origins has moved beyond intellectual debate in recent years and taken on the flavour of competing ideological crusades. There has been protracted academic huffing and puffing (especially wearisome to third parties), but little constructive dialogue: some exponents of the continuity and the replacement theories seem to pay scant regard to what the other camp says, and there has been talk of a paradigm crisis in this area (Williston and Clark, 1995). A framework for evolutionary change in which the punctuational mode predominates will obviously predispose one to viewing modern human origins as resulting from the speciation and replacement model, but even in these terms the region of origin and its timing remain obscure. Later Middle Pleistocene sub-Saharan Africa is favoured by many on both palaeontological and genetic grounds, but there are difficulties with this. The sub-continent is a remarkably central focus for origin within the framework of a theory that sees most evolutionary novelties originating in peripheral areas. While the region has yielded some of the oldest examples of modern morphology (Klasie's River Mouth; Border Cave; Omo [Kibish] 1), the immediately preceding archaic forms (e.g. Kabwe [Broken Hill]; Saldana; Laetoli 18 [Ngaloba]; Omo [Kibish] 2; Eliye Springs) are not convincing as immediate antecedents. In some respects the North African and Levantine evidence is more appropriate for such a role (the latter region also providing evidence of similarly early [80–100,000 years] broadly modern forms at Skhul and Jebel Qafzeh), as are later Middle/basal Upper Pleistocene crania from China, such as Dali, Jinni Shan and Xujiayao (Pope, 1991, 1992).

Genetic diversity and molecular evolution

Many genetic studies show African populations to be more variable than those elsewhere (but see below), and this has been taken to reflect their greater time depth, so providing support for an African

origin for *Homo sapiens*. However, such genetic data may in principle reflect antiquity back to the basic hominid-pongid split, and do not themselves resolve the dispute over the modality of recent human evolution. Much more relevant are the age estimates associated with the origin of particular genetic markers, based on the assumptions of a perfectly neutral, regular mutational clock, and with the allele frequencies resulting principally from genetic drift, mediated in some analyses by population bottlenecks and expansions.

Studies of mitochondrial DNA (mt DNA) have suggested an African origin for modern humans some 140–290,000 years ago (Cann et al., 1987), later refined down to 166–249,000 years, with a mean around 200,000 (Vigilant et al., 1991). However, these findings were undermined by the realization that the evolutionary trees derived from the genetic data that pointed to an African origin were not in fact the shortest (i.e. most parsimonious) trees. There are multiple shorter trees, some with an African and others with a non-African origin, but the place and branching sequence cannot be resolved because of the nature of the data set (Maddison, 1991; Templeton, 1992; Hedges et al., 1992).

More fundamental criticisms of these studies have been made by Templeton (1993), who concludes that the mt DNA data do not indicate Africans to be more variable than non-Africans, because inappropriate statistics were used; appropriate statistics reveal no statistically significant support for greater African variability or an African root. Templeton also criticizes the reasoning underlying the use of the molecular clock in these studies and the age estimates derived, and the assumption of mt DNA neutrality. Wallace (1994) and Ballard and Kreitman (1995) review evidence for selection affecting mt DNA variants and summarize mechanisms that may influence the observed distributions.

Even if neutral or near-neutral, the phenomenon of 'genetic hitch-hiking' (non-coding or neutral sections of DNA contiguous with other, functionally important segments of the molecule and so carried along by the selective forces acting on their neighbours) is likely to be an important influence especially on non-recombinant mt DNA where linkage is total. For similar reasons, hitch-hiking is also likely to be an important influence on the great bulk of Y chromosome DNA, present only in males (some recombination occurs between X and Y chromosomes at their extreme tips). Y chromosome studies offer the same advantages for tracking lineages as mt DNA, but up to now have yielded few data for a variety of reasons: the smaller number of surveys, the large size of the molecule (4000 times that of mt DNA), and the lower mutation

rates. What information is available suggests that African populations are not especially variable compared with others, but it is not currently possible to identify the region of origin of the ancestral pattern or dates of origin and dispersal (Jobling and Tyler-Smith, 1995).

Most other genetic surveys do point to greater variability in African compared with non-African populations. A recent example is a study of autosomal nuclear DNA by Tishkoff et al. (1996), who analysed allele distributions from two distinct types of closely linked non-coding sites on the short arm of chromosome 12. One is a short random repeat polymorphism (STRP) – a block of 5 nucleotides repeated 4–15 times; the other is a deletion of an Alu repeat. This is an example of a short interspersed nuclear element (SINE); the Alu repeat is specific to primates and especially common in the human genome, where it occurs about 750,000 times. Tishkoff et al. typed the haplotypes (i.e. the combinations of alleles at these two loci) in > 1600 individuals from 42 populations and analysed the resulting distributions; they found striking contrasts in the distribution patterns between sub-Saharan populations on the one hand, and North African and other regions on the other, with the former markedly more variable than the latter.

The Alu deletion is associated with a wide range of STRP alleles south of the Sahara but nearly always with just a single STRP allele in North Africa and the rest of the world. Tishkoff et al. interpret this result to mean a long antiquity for the allele in sub-Saharan Africa, but that the populating of North Africa and other continents occurred more recently from a single source. On the basis of the relative frequencies of the alleles either side of the Sahara, and using the neutral molecular clock principle, they calculate a likely maximum age of 102,000 years for the expansion of the Alu-chromosome outside Africa, with an upper bound of 217–313,000 years. While the age range does not greatly refine previous estimates, Tishkoff et al. argue that it is compatible with both the fossil evidence and the disputed mt DNA findings and, as autosomal recombinant data derived from both parents, the contrasting sub-Saharan and North/extra-Africa patterns provide some of the strongest evidence to date supporting a recent African origin for *H. sapiens*.

Between the extremes of modern human origin by speciation (in Africa or elsewhere) and complete replacement of archaics on the one hand, and multiregional continuity across the Old World from the Lower Pleistocene onwards on the other (see below), is a broad spectrum of interpretations differing in their emphasis on the interplay of population expansion, migration, hybridization, gene

flow, replacement, etc. These have acquired various appellations: 'Strong Garden of Eden'; 'Weak Garden of Eden'; 'Hybridization and Replacement'; 'Continuity and Assimilation', and so on. Aiello (1993) and Lahr and Foley (1994) provide useful reviews, as do the more detailed collections by Brauer and Smith (1992) and Nitecki and Nitecki (1994).

Other studies have focused on the significance of population size and structure in recent human evolution. Harpending et al. (1993) used the Wilson group's mt DNA data to investigate pairwise differences within and between populations and to compare these with distributions derived from computer simulation. Relethford and Harpending (1994) compared contemporary craniometric diversity with that predicted assuming equal effective population sizes in different Old World regions, and found Africans significantly more variable, and Europeans less variable, than predicted from the model. They therefore concluded that long-term African effective population size was three times that of any other region. Relethford and Harpending also estimated the magnitude and extent of migration between regions, finding Africa isolated from the other continents.

Both sets of studies are most compatible with a 'Weak Garden of Eden' model, i.e. initial appearance of modern humans in Africa, slow spread into other regions without significant growth in numbers, followed at a later date by rapid expansion from these relatively isolated daughter populations. Harpending et al. (1993) date the expansion to 40,000–50,000 years ago, coincident with the Upper Palaeolithic transition. The results are also marginally compatible with the regional continuity model (depending upon the severity and extent of population bottlenecks), but incompatible with the 'Strong Garden of Eden' model that posits simultaneous population expansion and dispersal out of Africa. These findings thus conflict with Tishkoff et al.'s chromosome 12 studies, which conclude just that.

Genetic evidence relevant to modern human origins is thus accumulating at a rapid rate – certainly more rapidly than the fossil specimens – but the picture revealed is inconsistent, contradictory and confusing. However, what the genetic studies have in common is their emphasis on mutation and drift as the primary influences on genetic diversity, and the significance of bottlenecking as an important factor in human evolution. If future work validates the main framework of neutral theory, it will provide another important source of evidence for the overriding significance of contingency in the ancestry of modern humans. In the meantime we seem to have reached an impasse, or at least a stand-off, in the replacement versus

continuity debate. Despite a good deal of reiteration of the basic evidence for, and the logic of, each theory by its supporters, there appears little immediate prospect of reconciling these conflicting views, or that definitive evidence will decisively resolve the issues in favour of one or other interpretation. Rather, it seems likely that future developments will substantially modify current views on modern human origins.

Summary

The main points of the above review can be summarized as follows:

1. The hominid and African ape clades probably diverged 6–8 Mya. The earliest hominid fossil specimen is the Lothagam Hill mandible (> 5.6 Mya). More complete remains post-date 4.5 Mya, with the most extended evidence from East Africa (Ethiopia, Kenya, Tanzania); that from South Africa is more abbreviated. The formation of the Rift Valley and attendant climatic changes were doubtless major influences on the origin and early radiation of hominids.
2. There is clear evidence of multiple species in the Pliocene hominid fossil record, with distinct species both within and between the two African regions. Even the earliest phase was evidently characterized by an array of forms rather than a single lineage, since the Lothagam and Tabarin fragments are more progressive than the later (4.4 Mya) and remarkably primitive *Ardipithecus* material from Aramis, Ethiopia.
3. The refined palaeoenvironmental evidence linking early hominids to woodland underpins and reinforces the morphological evidence by providing an ecological context of patchy, fragmented habitat distribution that would promote speciation.
4. There is evidence of parallelisms, both in the evolution of 'robust' australopithecine morphologies, and within the material assigned to early *Homo*. The latter group includes at least three contemporaneous basal species, so that the genus is polyphyletic.
5. A markedly speciose phase seems to have terminated some time after 1.5 Mya. An especially stable morphology (*H. erectus* s.l.) originates some time before this (?2 Mya) and persists relatively unchanged until 0.1–0.2 Mya.
6. Claims for the specific distinctiveness of early African *erectus* (*H. ergaster*) remain controversial and disputed. Certainly, characterizations of *H. erectus* as an exclusively Asiatic taxon appear wide of the mark, for while there are differing views on

the affinities of the relevant Turkana specimens, all agree that OH 9 (c. 1.2 Mya) conforms to a narrow definition of the species.

7. Recent claims for early (terminal Pliocene) hominid expansion out of Africa are problematic, with the chronological interpretation less than secure. Nonetheless, there is more secure evidence of hominids in western Asia by 1.4 Mya, the Far East by c. 1.2 Mya, and South East Asia at about the same time or slightly later. Human occupancy of Europe appears to be more recent (?c. 0.8 Mya).
8. Despite its peripheral and intermittently isolated location, the bulk of the Javanese hominid fossil record shows remarkable similarities to that of mainland Asia over the greater part of its span. There is evidence of local differentiation in the latest part of the sequence (Ngandong—?0.1 Mya).
9. Dating indicates that the latest continental *erectus* (ZKD upper levels; Hexian) overlap with early 'archaic *sapiens*' in Asia (Dali; Chaoxian; Xujiayao; Jinniu Shan), so supporting notions of species distinctiveness.
10. There is no definite evidence for *H. erectus* in Europe. Although of appropriate age, the Atapuerca TD6 specimens are too fragmentary for specific determination, and later, more complete material (e.g. Heidelberg, Petralona, Arago, Steinheim, etc.) differs from *erectus* in various ways, so that these fossils are usually assigned to 'archaic *H. sapiens*' or *H. heidelbergensis*.
11. Such specimens do, however, show certain features that point to regional differentiation and continuity from TD6 through to Neanderthals. Evidence from Sima de los Huesos, Atapuerca, suggests that at least some later Middle Pleistocene local populations were remarkably variable, with some individuals evincing a 'proto-Neanderthal' cranial morphology, others less obviously so.
12. Neanderthals themselves show distinctive features in consistent combination and reduced variability compared with the material referred to in (11) above, suggesting the outcome of a 'bottleneck' effect. It is difficult to account convincingly for all Neanderthal features as adaptive.
13. It is similarly difficult to account for all aspects of modern morphology as adaptive other than by the – to my mind unconvincing – 'general economy' argument. It is possible that many archaic-modern contrasts involve a significant degree of phenotypic (non-genetic and so non-evolutionary) lability. By extension, there is no reason in principle to exclude such

plasticity from contributing to earlier disjunctions in the fossil record, although it is perhaps likely to have been only a minor component.

14. There is no evidence that modern morphology confers enhanced fitness compared with that of Neanderthals. The disappearance of the latter may reflect extra-somatic (socio-cultural or technological) advantage on the part of early modern humans, which could, however, easily have originated the other way around. Alternatively, Neanderthals may represent a late archaic population in terminal decline, perhaps a consequence of the bottleneck(s) noted in (12). Their overlap with early modern humans in Central and Western Europe would then be fortuitous, and the appearance of the latter unconnected with, or only a very minor factor in their disappearance.
15. The place, timing and factors underlying the first appearance of modern morphology are obscure. Sub-Saharan Africa is the preferred region for many, but its preceding archaic morphologies are unconvincing as appropriate immediate antecedents. In some respects later Middle Pleistocene specimens from North Africa, the Middle East and China are better precursors for modern morphology.
16. The bulk of the data on contemporary genetic diversity point to an African origin, but the time-depth of this is currently unresolved. The significance of this evidence for reconstructing human evolution depends critically upon estimates of mutation rates, and the relative importance of genetic drift as opposed to selection, etc. – all of which are presently disputed. Current ideas on modern human origins are likely to require substantial modification as further evidence accrues.

The phyletic implications of the preceding sections are represented in Fig. 4.2.

Anagenesis and speciation

The presence of morphological disjunctions in the hominid fossil record points to multiple species in both the earlier, African phase and that documenting subsequent expansion to other continents. It is evident that the pattern of hominid phylogeny was appreciably more polyphyletic than many workers considered even half a decade ago, and certainly far more speciose than I had appreciated it to be. As noted above, such multiple species greatly increase the probability that contingency has been a significant influence in human evolution.

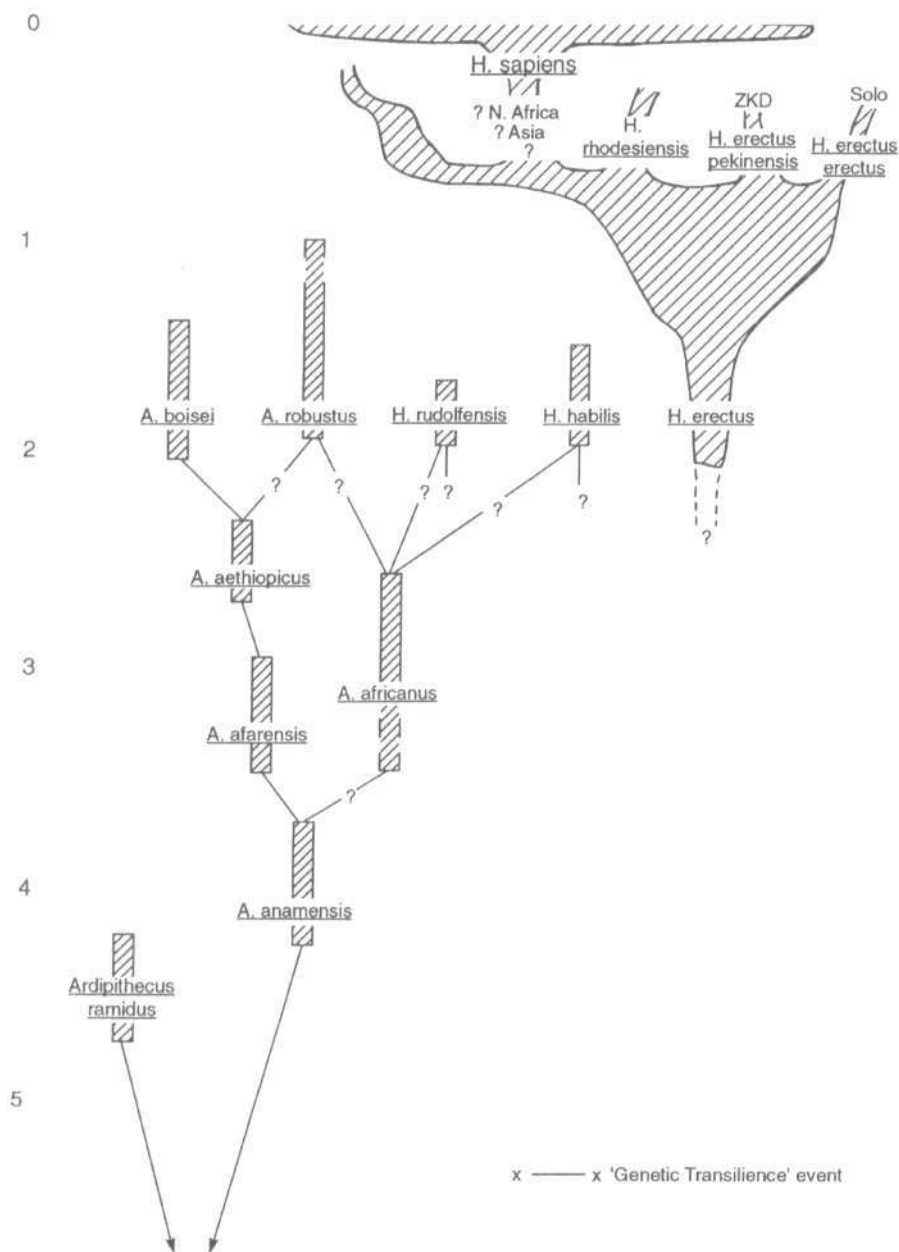


Figure 4.2 Proposed hominid phylogeny

Punctuational theory, together with studies of the genetics of small populations and of speciation mechanisms, provides a conceptual framework for such findings and the likely processes involved. Pliocene and Pleistocene hominids, living in small groups and thinly scattered across extensive areas with fragmented local habitats, can be expected to have closely conformed to many elements of Wright's 'shifting balance' model of small, semi-isolated populations, each one differentiated from the others by a combination of founder effect, drift resulting from intergenerational sampling errors, and local adaptations. Over time some demes (local populations) will become extinct and may, or may not, be replaced by others moving or expanding their range; yet others may coalesce with enhanced genetic and phenotypic variability. The upshot overall will be a dynamic, fluid situation at the local level, with appreciable but continually changing patterns of inter-demic variability in which stochastic factors play a significant role.

Gradual, directional change may from time to time characterize some limited parts of the species range, particularly if they are separated from the remainder, whether because the selection pressures are relatively widespread, or because chance effects combined with short-range gene flow may push several populations in the same direction. However, over the entire species range selection pressures are likely to vary considerably, while the distances and barriers involved will minimize the effects of gene flow. In the absence of any overall co-ordinating agent the outcome will be little or no directional change for the entire species – in other words, stasis. Regionally limited anagenesis may thus be apparent as an infra-specific phenomenon, and fully compatible with stasis at the species level (Eldredge, 1995), rather than presaging a transformation of the total gene pool.

The predominant source of longer term change is speciation, particularly peripatric speciation (Mayr, 1954), or variants of this (populations close to or at the limits of the species differ from those elsewhere because of genetic drift and distinctive selection pressures). A (geologically) short period of isolation will further accentuate differences due to founder effect and subsequent drift. Even if only a few genes with major effects are initially affected, selection will act on other parts of the genome (polygenic modifiers) to shift the character(s) to a new adaptive peak, so further promoting contrasts between the isolate and the original species (Templeton, 1980; and see below). The outcome is a new species.

Like some others, I had been troubled by the punctuational model's emphasis on the link between morphological change and speciation at the expense of anagenesis. After all, the latter has been

demonstrated not only in the fossil record but also through field studies, in many cases with clear and convincing links to directional selection pressures. And yet the clear implication of punctuation was that species could not respond to sustained directional selection other than by speciation, with apparent phyletic trends in fact resulting from differential rates of species origination and extinction (species selection or sorting). In the circumstances this seemed a perversely over-elaborate explanation to account for trends, and designed simply to accommodate the notion of stasis.

Futuyma (1987) has greatly clarified this issue for me (and, I suspect, others – see Gould and Eldredge, 1993) by pointing out that anagenesis is a continual but essentially ephemeral phenomenon. New, locally adaptive features may arise and become locally established, but in the longer term or on a larger scale are broken down by the recombination arising from migration and gene flow. In Futuyma's words:

Given reproductive isolation, however, a species can retain its distinct complex of characters as its spatial distribution changes along with that of its habitat or niche. Thus, speciation can facilitate morphological change, not by liberating a population from genetic homeostasis or accelerating the response to selection, but by enabling a gene pool to remain subject to consistent selection pressures even as it moves about in space. ... Although speciation does not accelerate evolution within populations, it provides morphological change with enough permanence to be registered in the fossil record. Thus it is plausible to expect many evolutionary changes in the fossil record to be associated with speciation. (emphasis added.)

Speciation thus promotes longer term trends by preventing backslippage during character transformation, so acting as an evolutionary ratchet: 'even without species selection in the sense of differential speciation and extinction rates, speciation may facilitate anagenesis by retaining, stepwise, the advances made in any one direction.' And, in an especially striking metaphor, 'If we envision an adaptive landscape. ... successive speciation events are the pitons affixed to the slopes of an adaptive peak' (Futuyma, 1987).

If Futuyma's analysis is correct, and if speciation is prompted by isolating agencies that have little or nothing to do with adaptation *per se*, then contingency lies at the very core of the macro-evolutionary process. For the pitons will be hammered in, not at points necessarily corresponding to the shortest or most accessible route up to the peak but randomly, according to the vagaries of isolation. And yet, as with mountaineering, the position of each piton determines the next phase of the climb. Persistent lineages (which are, in fact, species clusters rather than single lineages)

fortuitously happen upon an accessible route up the gradient, but many others must be ephemeral as a consequence of finding their route impassible, falling off the rock face to extinction. The ones we retrieve, and which form the basis for our perceived anagenetic trends, are the lucky ones.

Hominid range, ecology and speciation

While both the fossil record and population theory therefore point to speciation as a likely phenomenon during hominid evolution, there continues to be a contrast – reduced in scale when compared with phyletic schemes of the 70s and 80s but still evident – between the earlier (mid-Pliocene–basal Pleistocene), intra-African phase, and the later (Lower Pleistocene onwards) which, despite much extended hominid geographical range and associated habitat diversity, displays fewer clearly defined species.

As summarized above, relevant contextual evidence reinforces interpretations of contingent effects among early hominid species. Quite apart from the impact of geological factors (the emergent Rift) on East African hominids, the increasing contextual evidence of woodland habitats points to a much patchier, discontinuous distribution for *Australopithecus* than earlier, savanna-based reconstructions. If correct, this scenario reinforces the view that the recently recovered KT12 Chad hominid (Brunet et al., 1995) represents a new species of *Australopithecus*, *A. bahrelghazeli*. The KT12/H1 mandible fragment shows undoubted resemblances to *A. afarensis*, but these may reflect nothing more than primitive commonalities, and the specimen also possesses distinct features of the symphysis and dentition. However, given its fragmentary nature, zoogeographical considerations (its location is 2500km west of the Rift Valley) are powerful arguments for its specific distinctiveness.

Similarly patchy distributions are to be expected for other australopithecine and early *Homo* species, such as *H. habilis*, still tied to woodland. If anything, population fragmentation (and so species diversity) might be expected to have increased in the later Pliocene with evidence of drier, more open environments. Such conditions doubtless also intensified selection pressures for greater terrestriality in open environments, to which the postcranium of early *H. erectus* can be seen as a response. The appearance of this morphology, probably some time before 2 Mya, signifies a distinct adaptive shift (see below). Its initial evolution is quite unknown, and there is a lack of obvious precursors, but its success is evidenced by the expansion of *H. erectus* within and beyond Africa, well before 1 Mya.

However, as noted above, despite the much wider spatial and

corresponding ecological range, which might be expected to promote hominid speciation, morphological evidence of corresponding diversity is at best equivocal. The case for distinguishing early African hominids of *erectus* grade as specifically distinct from the Asian forms as *H. ergaster* (Wood, 1992), has attracted support from some workers, but also considerable criticism. Some aspects of the debate are influenced by contrasting approaches to phyletic inference, but this is certainly not the whole story. For example, while cladistic arguments have been advanced to support separation, Harrison, a palaeoprimatologist with much experience of cladistic methods for investigating Miocene catarrhine diversity, has criticized such analyses of the African and Asian *erectus* fossils that argue for species distinction, preferring to consider them as conspecific (members of a single species). The differences between them 'may be explained as populational differences, rather than post-speciational divergence' (Harrison, 1994, p. 364). Similarly, the South East Asian hominids, although biogeographically and palaeoecologically promising as exemplars of hominid speciation, fail to deliver the requisite morphological evidence thereof.

What the *H. erectus* record does appear to show is evidence of anagenesis. At the very least the Kabuh-Notopuro bed sequence in Java points to a regional trend of brain expansion and gracilization of neurocranial superstructures, while Zhang (1991) has documented regular temporal changes in the Zhoukoudian dental sample, so illustrating Eldredge's (1995) general statement about spatially limited trends. The presence or absence of such trends on a larger scale (i.e. species wide) is a moot point: Leakey and Walker (1976); Gould and Eldredge (1977); Stanley (1979); Eldredge and Tattersall (1982); Rightmire (1985; 1986a; 1986b) and, with qualification, Howell (1994) have all cited *erectus* as a clear case of stasis. Cronin et al. (1981); Wolpoff (1984); Bilsborough and Wood (1986); Bilsborough (1992) and Leigh (1992) have all argued for the presence of trends, with the clear implication of a single old-world wide polytypic species mediated by pan-continental directional selection pressures.

All this does not exclude the possibility – indeed, probability – of stochastic factors influencing local *erectus* communities and promoting inter-populational differences, but it suggests that the outcomes were of much reduced magnitude compared with earlier hominids, despite the more localized distribution of the latter. In effect, it suggests that they were confined to Gould's first explanatory tier (micro-evolution) rather than the second tier of species-level phenomena (Gould, 1985). I view this as strong presumptive evidence of distinct adaptive modes and strategies between earlier and later hominids.

Multiple, comparatively short-lived hominid incursions into higher latitude Europe and Asia with their unstable climatic regimes would further increase opportunities for random effects and group differentiation. Again, these might be expected to assume greater significance the longer the time-scale since initial entry. As summarized above, evidence of possible early migration into both continents is thin and shaky. The absence of clearly defined regional hominid varieties for the greater part of the Lower Pleistocene also argues against very early colonization, around the Plio-Pleistocene boundary, as do the similarities (conceded even by those who would recognize *ergaster*) between Asian *erectus* and all but the very earliest African specimens. The only way of reconciling this pattern with a long extra-African chronology would be to posit extensive, omni-directional gene flow – between centre and periphery, and also between peripheral populations – from a correspondingly early date. All this would run counter to what is known of the likely ecology and behaviour of Lower/early Middle Pleistocene hominids; it would, of course, also be incompatible with a punctuational interpretation of human evolution.

On the other hand, significant contrasts are indicated in the sub-Saharan record from the mid-Middle Pleistocene, and in the North African and Asian records from the later Middle Pleistocene. As noted above, the European evidence contains no *definite* evidence of *H. erectus*; more 'progressive' forms are clearly present from mid-Middle Pleistocene times, but earlier specimens, while evincing regionally distinctive features, are too fragmentary for their affinities to be established with confidence.

The African record of later *H. erectus* is relatively limited: the latest sub-Saharan specimens appear to be those from Bed IV Olduvai (0.7–1.0 Mya), and, possibly, the Baringo Kapthurin mandibles, probably between 0.3–0.5 Mya. The earliest 'archaic sapiens' specimens such as Bodo, Ndotu and possibly Kabwe are 0.2–0.4 Mya so that if the relatively late Baringo fossils are correctly assigned to *erectus*, overlap is suggested, but not conclusively demonstrated. If, on the other hand, the Kapthurin mandibles represent 'archaic sapiens', which is possible, then there is a significant temporal gap between this and *erectus*.

Evidence for temporal overlap is better documented in Asia. As reviewed above, the broad contemporaneity of *erectus* specimens such as Zhoukoudian upper levels and Hexian with Dali, Changyang and Chaoxian supports the interpretation of a speciation event. Later continental specimens such as Xujiayao, and Jinniu Shan also contrast with the Javan Ngandong crania, pointing up differences between the mainland and insular records.

Regional continuity within one part of the Asian *H. erectus* realm evidently led to a progressive form (morph) by isolation and anagenetic 'fine tuning', whereas speciation in another, more northerly part of the range resulted in even more progressive form(s) subsumed within 'archaic *sapiens*'. Whether the southern mainland morph represented by Maba and Narmada represents a further Asian species or intrusive migrants remains to be determined.

Evolutionary processes in the European fossil record

There is general agreement that the earliest well dated European specimens differ from *H. erectus* as known from Africa and Asia. For the last three decades these specimens have usually been assigned to 'archaic' *Homo sapiens*. More formal attribution has often been avoided, but when attempted has usually been at the subspecific level as either *H. sapiens steinheimensis* or *H. sapiens heidelbergensis*. Tattersall (1986, 1992, 1995) has severely criticized the extension of the modern human species to cover such diverse morphology, and there is growing recognition of the force of his arguments. In many ways *H. heidelbergensis* seems the most appropriate taxon for the Middle Pleistocene European material, and this has been proposed by Tattersall. However, he extends *heidelbergensis* to include broadly contemporary East African specimens such as Bodo, Kabwe and Ndutu, so diluting the morphological characteristics of the species, and also eroding the likely biogeographical underpinning of the population differentiation. Since the European and sub-Saharan fossils show distinct morphological patterns (in my view the contrasts considerably exceed those between African and Asian *H. erectus*) specific distinction appears justified, with the African forms as *H. rhodesiensis*.

This leaves *H. heidelbergensis* for the European fossils, but there remains another issue. Most, if not all of these specimens display one or more autapomorphic features (derived characters uniquely defining a lineage) associated with Neanderthal fossils from the Upper Pleistocene, although usually not in the consistent combination that characterize the latter group. On this basis inclusion of all European fossils (Middle as well as early Upper Pleistocene) in *H. neanderthalensis* is viewed by some workers as most appropriate. This taxonomic wrangle exemplifies more substantive issues about the processes and patterns of human evolution. Given the distinctive nature of the European Middle Pleistocene fossils, do Neanderthals represent a further distinct, relatively recent and short-lived species originating post-*heidelbergensis*? Alternatively,

are they the terminal, anagenetic outcome of a European-west Asian human clade subject to strong and prolonged directional selection, and with its roots in the early Middle Pleistocene? Or are they the intraspecific products of micro-evolutionary processes – sampling errors and what might be termed ‘constrained directionality’ – i.e. selection interacting with reduced phenotypic variation?

The first of these (Neanderthal origination by speciation) accords with an extreme punctuational view of human evolution and has recently attracted support from some workers, but is difficult to demonstrate with any confidence, although more extensive Mid-Pleistocene postcranial remains may support it if they turn out to contrast with Neanderthal postcrania. The second, gradualist, interpretation posits sustained phyletic change, viewing Neanderthals as resulting from similar evolutionary processes as those described for the Ngandong population. There is, however, a fundamental difference between the two cases: Ngandong represents the localized phyletic transformation of some (not all) *erectus* populations; if the specific distinctiveness of the European hominids as *heidelbergensis* is accepted, then on this model Neanderthals would represent transformation of the entire species or lineage. This controverts the punctuational notion of species as essentially static, and a whole-species shift is difficult to square with the contracted variability of the later fossils compared with the earlier specimens. Of course, one way to make the two cases comparable is to extend *heidelbergensis* beyond Europe, as Tattersall has done, but that not only runs counter to the morphological evidence (see above), but effectively destroys the second model, transforming it instead into a particular case of the third.

In fact, the third interpretation appears to me the most plausible, given the particular character set of Neanderthals and their restricted internal variation compared with the wide intra-populational range of the Atapuerca and other Middle Pleistocene hominids. On this view the European fossils would all be accommodated within *Homo neanderthalensis* on grounds of taxonomic priority, but Neanderthals *per se* would be atypical of the species overall due to bottlenecking effects. Stanley (1979) argues against the importance of bottlenecks generally as a major source of longer term (palaeontological) change, but in my view the fossil evidence points to the phenomenon in this particular instance.

Carson (1975, 1987) and Templeton (1980) have both provided modifications of Mayr's (1954) peripatric speciation model that posit more restricted change in the peripheral demes than Mayr originally envisaged, and which accommodate bottlenecking and its evolutionary consequences. Carson argues that species' genomes

are normally highly organized, co-adapted and hence stable; speciation can only occur following destabilization of the existing system. A drastic reduction in population size is one such, randomly occurring, destabilizing mechanism. 'A new species may be formed if the deme and its descendents can emerge from this critical, disorganized genetic state and be subject to renewed selection. It is proposed that this renewed selection will take the form of strong directional selection toward a novel character set' (Carson, 1987).

Templeton, in particular, emphasizes the importance of changes in a few genes (particularly those with major phenotypic effects that act as modifiers) rather than many for promoting speciation, preferring for that reason the term 'genetic transilience' to Mayr's original 'genetic revolution' to describe the phenomenon. Following Mayr, he stresses that small isolates will not only deviate in their gene frequencies from the parent population, but will also show reduced variance and higher inbreeding. This will more readily expose homozygotes (identical genes inherited from both parents) to selection, favouring those genes that are fittest in homozygous combination. The number of genes involved may not be large, but because of interactive (epistatic) and developmental effects, there is interaction between loci that may result in a snowballing process before reaching a new, co-adapted, stability: changes in one or more genes (the genetic environment) may significantly affect the selective value(s) of others.

genetic transilience is ... a rapid shift in a multilocus complex influencing fitness in response to a sudden perturbation in genetic environment ... genetic transilience can lead to both pre- and post-mating isolation from the ancestral population, as well as differences in morphology, life-history, development, physiology, etc. ... the shift in genetic environment (which can be caused by the founder effect) directly leads to the altered selective conditions that, in turn, cause the transilience and speciation. This serves to distinguish speciation *via* the founder-effect genetic-transilience model from gradual, adaptive, allopatric speciation (i.e. due to geographical separation): in the former case, the act of isolation itself leads to an altered genetic environment that *causes* the speciation event to occur; in the latter, the act of isolation merely *allows* speciation to occur as a by-product of ordinary micro-evolutionary processes. (Templeton, 1980)

This second process is the kind described by Futuyma (1987) and referred to above.

Templeton goes on to model transilience under differing assumptions about parental population size and structure. He shows that the probability of transilience is high if the parent population is large, unsubdivided and randomly mating (panmictic),

and low if it conforms to Wright's classic island model of many small demes with minimal gene flow between them, so that the founder population is derived from one such isolated deme. Both of these models are probably relatively unrealistic in describing the structure of Upper Pleistocene human populations.

However, Templeton also models transience assuming a 'Yanomama' population of changing demes structured by kinship and with extensive gene flow between – a pattern characteristic of many small groups of modern hunter-gatherers and shifting cultivators, and also some non-human primates – and so a likely better approximation of later Pleistocene population structure. With this situation the probability of transience is moderately high if the founders are drawn from a single deme, and higher still if they are drawn from several demes, which is again a more realistic scenario.

It seems to me that Templeton's model may very well describe the situation of European/west Asian human groups around the Middle/Upper Pleistocene boundary, and account for both the reduced variability of Neanderthals compared with antecedent populations, and for their distinctive features. Both follow from the greater homozygosity consequent upon a bottleneck of some kind, with the changed genome itself a component of the selection pressures to which the founder individuals are subject. In particular, the characteristic Neanderthal cranial and postcranial skeletal morphology may well result from selectively interacting genes at 'loci regulating fundamental developmental, physiological and life history processes'. In this way relatively limited genetic changes may produce widespread changes throughout the skeleton because of multiple effects (pleiotropy) and interaction (epistasis). This does not exclude a role for phenotypic lability (see above) and, in a sense, the precise level of its contribution is an irrelevance, since the capacity for such lability is genetically determined, and no-one, so far as I am aware, would ascribe *all* Neanderthal features to exclusively phenotypic modification.

Both Carson and Templeton provide their models in the context of speciation processes. As indicated above, the evidence does not convince me that Neanderthals were specifically distinct from earlier European populations such as those represented by the Atapuerca, Arago, Biache, etc. fossils, although a bottleneck and genetic transience might have sent them well on the way to reproductive isolation. However, I can see no reason in principle why such processes cannot have been responsible for the observed fossil patterning while being insufficiently sustained or intense to result in full speciation. There are no examples of the older morphology persisting into the European Upper Pleistocene and co-

existing with Neanderthals, which again suggests a contraction and shift within a single lineage rather than a speciation event.

However, there is, of course, good evidence for the contrasting morphology of *H. sapiens* contemporary with Neanderthals (and also, although less certain, suggestions of contemporaneity with other archaics, e.g. the contrasting morphologies of Omo [Kibish] 1 and 2). Whether modern humans originated in another region from a transilience event or by 'conventional' anagenesis following isolation is unknown, but the process surely involved different parent populations, different alleles (not just allele frequencies) and possibly different loci. Other Middle Pleistocene fossils lack the characteristic features of the European fossils, so indicating a parental gene pool for the founding population of *H. sapiens* distinct from that of the Neanderthals. In addition, the two daughter groups show contrasting morphological patterns, both with each other and with their inferred parents.

Both groups possess cranial features that are distinctive and derived, although in contrasting ways. However, while *H. sapiens*' postcranial morphology and proportions appear to resemble those of earlier specimens, showing few changes other than gracilization, those of Neanderthals show more extensive contrasts in trunk and limbs with the Lower/Middle Pleistocene evidence. The postcranial traits are doubtless linked genetically with Neanderthal cranial features, and phenotypic lability may again play a significant role in their expression, but the contrasting patterns and their extent in the two groups – cranially restricted on the one hand, more diffuse on the other – point to their differing genetic bases, whether extensive or limited to a few loci, strongly or weakly heritable.

Studies of extant forms demonstrate that morphospecies and biospecies are not always precisely congruent, but the former provide the only evidence available for palaeontology to identify the latter. Even if pan-continental species integrity within *Homo* was maintained until the final Middle Pleistocene (which I do not now believe to have been the case), so that both *H. neanderthalensis* and *H. sapiens* were no more than infra-specifically differentiated from their parent populations, then effective reproductive isolation could still obtain between the daughters, particularly if a transilience were involved. Some minimal genetic leakage, perhaps via intermediates, would not necessarily invalidate a general pattern of separate and distinct gene pools for sporadically adjacent populations characterized by differing, disjunct morphologies. Certainly the Levant evidence appears consistent with this view.

Fig. 4.3 attempts to model later hominid phylogeny, taking account of the processes and mechanisms summarised above.

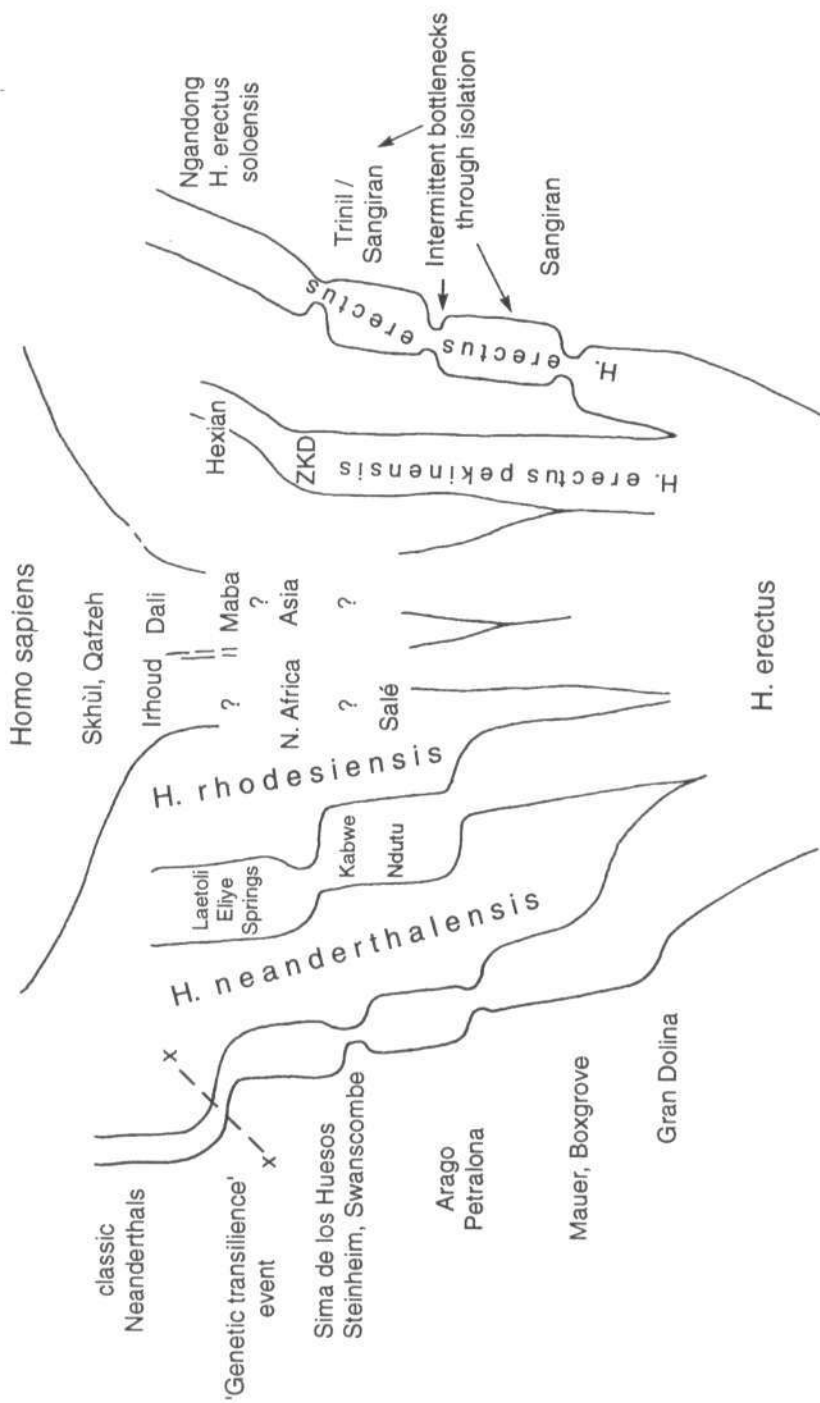


Figure 4.3 Proposed later hominid phylogeny

Competing models of human evolution

Interpreting hominid evolution within a punctuational framework highlights the probable roles of stochastic factors and contingencies as significant influences. The alternative, of course, is the gradualists' deterministic model of a single lineage evolving on an Old World-wide basis towards modern human morphology. Examples of anagenetic interpretations include Wolpoff, Wu and Thorne (1984); Tobias (1991); and Bilsborough (1992). The most recent, and in some respects most extreme, comprehensive restatement of this view is by Wolpoff et al. (1994). They argue for an exclusively anagenetic mode for later hominid evolution, and a single polytypic species since the origin of *H. erectus*. Given this framework and the difficulty of defining *H. erectus* and *H. sapiens*, they therefore propose sinking the former within the latter, which on this view as an evolutionary species, extends over the last two million years (see Fig. 4.4).

Its origin is in a cladogenic event that is at least 2.0 myr. We view the subsequent lineage as culturally adapted to an increasingly broad range of ecologies, ultimately leading to its spread across the world some half or more million years later. *Homo erectus*, the name generally accepted for our lineage in the Early Pleistocene, differs from contemporary *Homo habilis* in a number of ways. The vast majority of these distinctions also characterize *Homo sapiens*; that is, the diagnosis of *Homo erectus* relative to *Homo habilis* largely characterizes *Homo sapiens* as well. Every one of the few characters that are not shared appear to change in response to the evolutionary trends of increasing cultural complexity, increasing brain size, and the progressive substitution of technology for biology. *Homo erectus* thus is not a static species. It shows a number of evolutionary trends in the direction of *Homo sapiens*.

Moreover, *Homo erectus* is a polytypic species, divided into several distinct geographic variants which show continuity with the geographic variants of the polytypic species *Homo sapiens* through the sharing of unique combinations of morphological features. There is no distinct boundary between *Homo erectus* and *Homo sapiens* in time or space.

That is, there is no evidence of an appearance of a new combination of features separating earlier and later populations in one area (which contrasts with the events at the origin of *Homo erectus*). The characteristics of *Homo erectus* and *Homo sapiens* are mixed in transitional samples that are found in the later Middle Pleistocene of every region where there are hominid remains. We interpret these data to mean that there is no speciation event involved in the emergence of *Homo sapiens* from *Homo erectus*. The absence of a cladogenic event creating a distinct boundary at the 'origin' of *Homo sapiens*, together with the related patterns of polytypism in both 'species', provides an

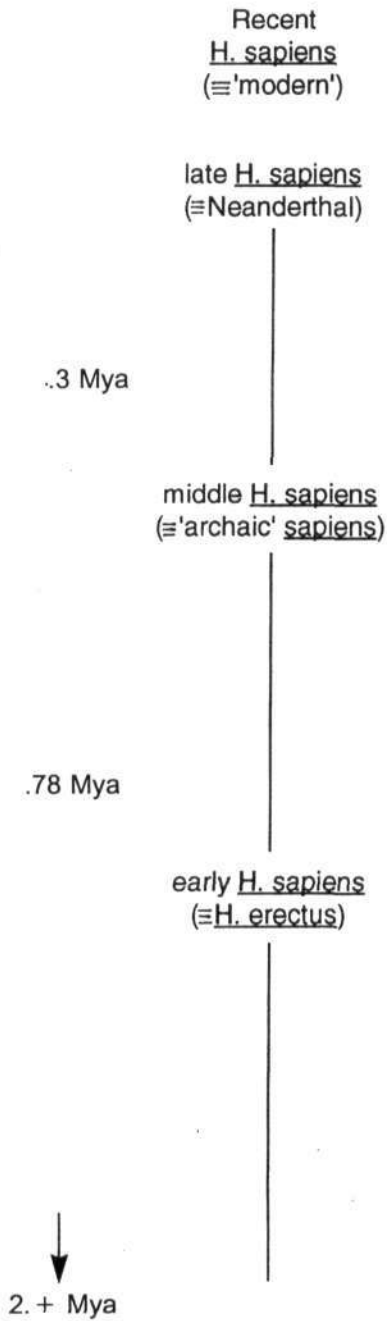


Figure 4.4 Later hominid phylogeny: Wolpoff et al. (1994)

explanation for the inability to develop a valid morphological definition of *Homo sapiens*. These reasons combine to require that the lineage be regarded as a single evolutionary species.

We view this evolutionary species as spanning the entire Pleistocene. The species is geographically polytypic once human populations begin to migrate out of Africa, 1.4–1.2 myr. This polytypism is characterized in morphological combinations which include (but are not restricted to) a number of features we believe are used in kin recognition. The main evolutionary tendencies in the species are linked to the evolving cultural system and its role as both a cause and an effect in what we regard as the human biocultural evolutionary process.

... We believe the notion of *Homo sapiens* as a single evolving species throughout the Pleistocene makes clear the central distinguishing feature of human behaviour – the unique nature of biocultural feedback as the mechanism driving our learning, adaptation, and social organization. (Wolpoff et al., 1994, p. 355)

Despite the authors' protestations to the contrary, this is, in effect, the single species hypothesis in a refashioned form. It necessarily presupposes constancy of selection pressures on hominid populations, not only across the whole of the Old World, but also over the entire span of the Pleistocene. More particularly, it envisages a predominant and stabilizing influence for those pressures associated with socio-cultural acquisition and elaboration. The entire hominid evolutionary process over the last two million years is seen as progressive fine tuning to such a niche. The counter view has been clearly put by Eldredge:

Most species ... are distributed over large regions. ... There are invariably a multiplicity of different habitats within such large areas, and no species will be found in all habitats. The result: Species are inherently and necessarily disjunct in their distributions. ... Local populations of a species will be integrated into local ecosystems, and each ecosystem will differ somewhat from the next. ... Now, imagine a species persisting as geological time rolls by. Each population represents a sampling of the genetic information in the species. Each is in different ecological circumstances. The effects of drift and especially natural selection will be different in each semi-isolated population. As. ... environmental conditions change, the effects will be different from one population to the next. ... Given this picture of the organization of species, it defies credulity that any single species, as a whole, will undergo massive, across-the-board gradual change in any one particular direction. After all, its component populations are all having semi-independent histories, some going one way, some another, others yet another. There is no way the entire species can march off, all demes united, on a single evolutionary pathway. (Eldredge, 1995, p. 83).

These two quotations encapsulate totally contrasting views of the selective influences and processes involved in human evolution. At a more mundane level of analysis, the very scale of the morphological contrasts between early *H. erectus* and modern *H. sapiens* argues against constancy of niche and selection pressures as envisaged by Wolpoff et al., quite apart from the difficulty in accepting that a period of two million years characterized by the environmental fluctuations of the Pleistocene could ever be regarded as effectively constant.

Conclusion

To assert a significant role for contingency in hominid evolution is to make a pretty unexceptionable statement, and it is not difficult to envisage scenarios in which stochastic effects were appreciable. It is much more problematic to identify fossil evidence that convincingly points to such instances and, as we have seen, some of the theoretically more promising cases turn out to offer little or no indication, even though in principle expanded geographical range offers many more opportunities for such effects.

Nonetheless, it has become apparent that human evolution was evidently more speciose than I had appreciated it to be, with correspondingly greater scope for contingency. It was particularly bushy in its earlier phase, but even the later hominid record shows patterning that is difficult to reconcile with a simple monophyletic interpretation. The account presented here, and the pattern it implies, therefore differs appreciably from my earlier accounts (e.g. Bilsborough, 1992). While moving toward additional species recognition, I have attempted to conform to the principle outlined in the introduction of incorporating only the minimum array required for compatibility with the relevant fossil evidence. My preferred scheme is therefore less polyphyletic than some others (e.g. in not differentiating between African *H. ergaster* and Asian *H. erectus*), and accords a significant, albeit reduced, role to anagenesis (e.g. in accounting for temporally related change in *H. erectus*, prior to regionally based speciation). As noted above, I also regard the bottleneck-transilience event that possibly underlies the evolution of Neanderthal morphology as an example of anagenesis, although of a rather unusual and distinctive kind.

The personal and subjective element is particularly prominent in judgements such as the above; others have reached and will, quite legitimately, continue to reach different conclusions about the processes influencing human evolution, and so the phyletic schemes they proffer. Whatever the differences of detail, it seems clear to me

that any really adequate scheme has to accommodate the twin aspects of diversification (speciation) and phyletic change (anagenesis) – hence the quote from Gould and Eldredge (1993) heading this paper. Too many interpretations have stressed one mode at the expense of the other. Excessive species recognition fails to take adequate account of intra-specific variability as a major contributor to fossil diversity and promotes a fragmented, typological view of phylogeny that is incompatible with known evolutionary processes. Unjustified assertions of monophyly have their own unrealities and pitfalls. The earlier quote from Eldredge (1995) effectively summarizes these, but the image conjured by some single species accounts is less an army of marching demes than a flotilla of old, pre-dreadnought battleships, sluggish of response and slow of manoeuvre. Such constructions might be just adequate in a homogeneous oceanic-like environment, but it seems unrealistic to view them as persisting successfully in varied, fluctuating conditions.

If the models preferred here at all approximate to the reality of human evolution, then contingency lies at its heart: contingency in the timing and intensity of the isolating or bottlenecking mechanisms; contingency in the size, composition and characteristics of the founding population that is isolated or preserved; contingency in the composition of the gene pool that is sealed off by the speciation process and, in the transience model, contingency in those parts of the genome that contribute the genetic environment for a particular gene complex with major developmental effects.

All the above elements are part and parcel of an interpretation of hominid phylogeny within a broadly adaptationist paradigm. However, the rapidly expanding data on genetic diversity and molecular evolution in contemporary populations provide much evidence for neutral evolutionary theory, and point up additional evidence for the predominance of contingency in human evolution, emphasizing the importance of mutation and genetic drift – both random processes – at the molecular level. Some genetic studies can be criticized for *assuming* neutrality and an exclusive role for drift, and selection is undoubtedly influencing frequencies in some instances (see discussion above, and especially Templeton [1993]; and Kreitman and Akashi [1995]). The interplay and relative importance of these factors for longer term evolution are currently disputed.

However, it is also clear that a pan-selectionist or exclusively adaptationist interpretation is also inadequate to account for the observed data: the diversity within and between populations is too

great to result solely from selection, and some studies (e.g. Tishkoff et al., 1996) demonstrate genotype variants to accord with Hardy-Weinberg expectations, implying absence of appreciable selective influences. Even on a neo-Darwinian interpretation, the genetic data stress the importance of small breeding population size – characteristic of human groups for much the greatest part of their (pre-) history – as a major evolutionary influence. It appears an inescapable conclusion that chance has played a major role in our make-up and in our evolutionary success.

There is, moreover, one additional and incontestable case of contingency exerting a predominant influence on the pattern of human evolution. The recognition and recovery of the fossil evidence are subject to vagaries beyond control, and the sequence of discovery as well as the extent of the evidence determine both our understanding of the detail and the conceptual frameworks within which we evaluate new discoveries. Few can doubt that if, say, the East African evidence had been discovered before rather than after the European Neanderthals, Asian *Homo erectus* and South African australopithecines, then not only the fundamental taxonomic units but also the phyletic patternings derived from them would be very different from those currently employed. In that sense, if no other, contingency is not merely one, but the predominant, influence on the pattern of human evolution.

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I am very grateful to John Bintliff for inviting me to participate in the symposium on contingency at the 1993 TAG conference, which stimulated the reading and subsequent shift of view reported here. It provides another personal example of the significance of contingent influences, albeit at the micro-conceptual level. I wish to acknowledge the stimulus provided by Stephen Gould's and Niles Eldredge's writings; Alan Templeton's publications for insights on molecular evolution and the genetic processes underlying speciation; and, for the evaluation of hominid diversity, the papers of Ian Tattersall.

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5 The human evolutionary time-scale and the transition between hunting and gathering, and farming

Robert Layton

Summary

This chapter will consider why it is that the transition between hunting and gathering, and farming, looks intuitively like linear progression, and what evidence can be put forward in favour of the alternative view that it is a cyclic process driven by human responses to random variation in the environment. Initially I shall present a revised statement of a detailed approach offered in a joint paper in *Current Anthropology* in 1991 (Layton, Foley and Williams), taking account of subsequent critical comments, and the computer simulation run by Winterhalder and Goland (1993). In the second part of the chapter, I will address the question – why did farming (or some parallel strategy) not occur earlier in prehistory?

The transition between hunting and gathering and cultivation has traditionally been presented in archaeology, and is still popularly regarded, as an evolutionary progression. As Gordon Childe put it, 'The escape from the impasse of savagery was an economic and scientific revolution that made the participants active partners with nature instead of parasites on nature' (Childe, 1942, p. 55). Twenty years later Braidwood and Willey put forward a similar view, arguing that agriculture was the end product of a long process of readaptation and intensification, prior to which 'culture was not ready to achieve it' (Braidwood and Willey, 1962, p. 342). A faint echo of this interpretation can be found in a recent paper by McConiston and Hole, who argue that the origin of agriculture depended upon the conjunction of a repeated climatic phenomenon with specific cultural practices that had previously been unknown, namely a social system based upon delayed return. 'These lands provided ample food only to people sufficiently prepared to respond to instability' (McConiston and Hole, 1991, p. 59). Yet this approach is out of tune with the prevailing neo-Darwinian premise that there is no absolute progression in evolution, merely a process of adaptation to particular niches. To what extent is it possible to explain the appearance of cultivation as an adaptive strategy within a neo-Darwinian framework?

Two years before the conference on which this volume is based Robert Foley, Elizabeth Williams and I published a paper in which we attempted to provide a general model for interpreting the transition between hunting and gathering and cultivation as one possible outcome of an essentially cyclic process, and to specify the ecological conditions under which the transition might occur (Layton, Foley and Williams, 1991). Since the paper's publication both Hawkes and O'Connell, and Winterhalder and Goland, have made valuable refinements and amendments to the argument we presented, which will be summarized below (Hawkes and O'Connell, 1992; Winterhalder and Goland, 1993). Neither we, nor those who responded to our paper, have addressed what seems a crucial question if the process is truly cyclic. Why did the transition to cultivation not occur earlier than 10,000 years BP, if it did not depend on an evolutionary progression? The present paper will attempt to answer this question.

The broad diet of hunter-gatherers

The paper by Layton, Foley and Williams (1991) drew together several well-known observations on hunter-gatherer and farmer subsistence. It was noted first that hunter-gatherers, especially in low latitudes, have a broad diet, similar in breadth to that of the

chimpanzees of Gombe reported by Teleki (1981). The Gidjingali of North Australia forage for 120 species of fish, shellfish and crustacea, 50 species of land animal and bird, at least 13 species of fruits and nuts, 6 species of root and tuber, and honey (Jones, 1980). Comparable ranges are reported for the Aché of Paraguay (Hawkes, Hill and O'Connell, 1982) and the !Kung of the Kalahari (Lee, 1968).

All three studies recognize that not all potential foods are of equal value as a means of subsistence. Hawkes, Hill and O'Connell demonstrate this in greatest detail (but see also Jones and Meehan, 1989 for further information on the Gidjingali), through a careful application of optimal foraging theory. Optimal foraging theory predicts which potential foods a hunter-gatherer should exploit and which (s)he should disregard because they give too poor a rate of return. The relative value (i.e. rank) of a resource is based on the costs and benefits of exploiting the resource when it is encountered. Its contribution to the diet depends on the frequency with which it is encountered. The theory predicts that the forager will disregard any potential food encountered whose rate of yield is lower than the average yield the forager is currently achieving. Thus, for example, Hawkes et al. calculate that the Ache achieve an average rate of return for their foraging activities of 1115 kilo calories per hour. Palm fruit, which only yield 946 kilo calories per hour, are only exploited at the end of a bad day's foraging. This is consistent with the theory's predictions.

The highest-ranked resources in the hunter-gatherer diet are typically game animals. Cultivators, on the other hand, concentrate their efforts on the husbandry of foods which lie at the lower end of the hunter-gatherer's optimal diet. Plants like the palms which are on the margins of the Ache diet are cultivated by horticulturalists such as the Nuaulu (Ellen, 1988), the rice and *ipomoea* [sweet potato] which the Gidjingali sometimes gather are staples in South East Asia and Polynesia (Jones and Meehan, 1989), and the wild grasses whose seeds are most time-consuming to gather in central Australia include several species of *panicum* [millet] (Yen, 1989; Cane 1989).

A cyclic model

In 1962 Wynne-Edwards published a general study of the mechanisms by which population regulation is achieved in a wide variety of species. Wynne-Edwards argued that populations regulate their numbers through the evolution of mechanisms *at the level of the group* that tend to prevent some individuals from reproducing in times of plenty and thereby threatening the group's food supply in subsequent times of shortage (Wynne-Edwards,

1962). This theory found its way into hunter-gatherer studies and was expressed in the view that hunter-gatherer communities rely on cultural mechanisms such as infanticide and taboos on intercourse during lactation to hold their population density below the carrying capacity of the land (e.g. Binford, 1971, p. 37). In Binford's view, Wynne-Edwards had demonstrated that hunter-gatherer populations could not be directly controlled by the availability of food. There could, therefore, normally be no adaptive pressure favouring techniques such as cultivation that increase the food supply (Binford, 1971, p. 39). Binford concluded that it would take the arrival of groups from elsewhere, displaced by rising sea levels after the last glaciation, to increase populations in the Near East to such a density that agriculture became necessary.

The fallacy of the Wynne-Edwards theory is discussed by Trivers (Trivers, 1985, pp. 81-5). It supposes that individuals will forego the advantage provided by an opportunity to reproduce, for the good of the population to which they belong. To overcome the limitations of models derived from Wynne-Edwards, we took as our second point of departure a cyclic model of the relationship between hunter-gatherers and their foods, originally devised by Foley for teaching on the course *Hunters and Gatherers Past and Present* at Durham University. If hunter-gatherers conformed to the typical pattern among non-human predators (for examples see Krebs and Davies, 1984, p. 101 and Trivers, 1985, p. 85) then, when high-ranked resources are abundant, the predator population increases in direct response to the higher carrying capacity of the environment. This leads to over-exploitation of prey and, as the rate of return from high-ranking prey falls, the predator has to rely increasingly on low-ranking resources. Since this reduces foraging efficiency we anticipated that members of the predator, that is the hunter-gatherer, population will be subjected to various stresses such as malnutrition and increased infant mortality which cause the population to decline. Once this has occurred, high-ranking prey resources are able to regenerate and the cycle begins again. In our original paper we referred to high-ranking resources dropping temporarily out of the optimal diet, but Hawkes and O'Connell pointed out that predators will always exploit high-ranking prey if they chance to encounter them (for further discussion of this point see Layton and Foley, 1992).

Reversibility

Our third observation was that the transition from hunter-gatherer to cultivator or pastoralist is not necessarily irreversible. The Kubu

of Sumatra, for example, alternate between foraging and cultivation (Sandbukt, 1988), while individuals can move between the Dorobo hunting and gathering community of East Africa and neighbouring pastoralists such as the Samburu or farmers such as the Kikuyu (Hodder, 1982, pp. 87, 97-8; Chang, 1982). Many societies have a mixed hunter/gatherer-cultivator mode of subsistence. Why, then, should there be an apparent tendency for farming to replace hunting and gathering in the long-term archaeological record?

Deviations from the model

We considered tendencies that might interfere with the expected progression of our cyclic model. Hunter-gatherers who have become sedentary in the recent past may experience rapid population increase. Lee (1980) has recorded this phenomenon among the !Kung and Jones (1980) among the Gidjingali. The increase is apparently made possible by circumventing the mechanisms which are thought to control hunter-gatherer population density. Body fat levels and duration of breastfeeding have been argued to control ovulation rates, while infanticide may be practised if carrying young children reduces a woman's ability to forage effectively (for recent summaries of the evidence see Ellison et al., 1993; Panter-Brick et al., 1993; for earlier studies see Cohen, 1980; Lee, 1980; and Ripley, 1980). It is not necessary to appeal to Wynne-Edwards' theory of group selection to explain this tendency, since the adaptive value of all these mechanisms for the mother and her other offspring can be demonstrated. Sedentism may allow body-fat levels to rise, eliminate the postulated inducement for infanticide and, through the introduction of more easily digested foods, may allow a shorter period of breastfeeding.

In his comments on our original paper Smith rightly pointed out that enforced sedentism among recent hunter-gatherers does not provide a close parallel with the conditions created by early farming (Smith, 1991, p. 269). Variation in ovulation rates in response to nutritional status and work patterns is now regarded as the outcome of natural selective processes which enhance women's lifetime reproductive success. The mechanisms operate within all human populations, in response to various ecological and behavioural variables (Ellison et al., 1993, p. 2248). Research on the effects of competitive running and recreational jogging showed that both activities tend to reduce ovulation rates among Western women (Ellison et al., 1993, p. 2249). High mobility among hunter-gatherers might have the same effect. Demanding agricultural work and seasonal food shortages among farmers, however, also reduce

ovulation rates (see also Panter-Brick et al., 1993). A comparison of Lese farmers and Efe hunter-gatherers in the Ituri Forest showed that the hunter-gatherer women were *not* subject to the nutritionally induced seasonal variations in ovulation rates which affected Lese farmers (Ellison et al., 1993, pp. 2248-50). More detailed comparisons of hunter-gatherers and farmers would be needed to identify the distinctive effects of a foraging mode of subsistence.

Our cyclic model predicted that reliance on low-yielding resources will increase nomadism. We argued that if the low-ranking resources brought into the diet were dense and predictable in their distribution, nomadism would, on the contrary, be reduced. We suggested this would be the case if the depletion of high-ranking resources led to an increased dependence on wild grasses. Hunter-gatherers are often portrayed as universally given to sharing and reciprocity, customs which are interpreted as precluding husbandry of game or crops (Ingold, 1980, p. 88ff; Ingold, 1988, p. 277ff; Endicott, 1988, p. 127). We argued that, contrary to the initial model, if grass stands were dense and predictable in their distribution, the population would respond through the territorial defence of resources, sedentism and increased husbandry.

In our view, farming is only 'better' in the strictly Darwinian sense if it allows the population pursuing this strategy to increase faster than that of hunter-gatherers competing for the same resources. As long as sufficient wild resources remain, the possibility of reverting to hunting and gathering remains open. The increase in the size of populations engaged in farming will, however, increasingly preclude reversion to foraging as wild resources are displaced by cultivated crops. This effect, we argued, is responsible for the apparent uni-directionality of the transition from hunting and gathering to farming in the long-term archaeological record.

Modifications and additions to the model

O'Connell and Hawkes argue that increasing the breadth of the diet by incorporating lower ranked resources will inevitably reduce the time the forager spends searching for those of high rank and therefore always enable the foragers to reduce their mobility. The forager population will, however, only increase if the techniques for extracting food from resources improve (Hawkes and O'Connell, 1992, p. 64). Winterhalder and Goland argue that the sustainable yield of resources is as important as the net rate of return, and provide a more comprehensive, dynamic model of the costs and benefits of foraging. They use a computer

simulation to demonstrate that forager population density will drop if a low-ranked resource is added to the diet which has a low density and/or a low intrinsic rate of increase. Forager population density will increase if a low-ranked resource (such as wild grasses) is added which has a high density and/or a high intrinsic rate of increase. They argue that neither sedentism nor the defence of territories need be invoked to predict this effect. Nor, it may be added, would it be necessary to invoke improved technology or storage to explain the success of the strategy. Winterhalder and Goland have provided a key dimension missing from our original paper, namely a sufficiently rigorous formulation to allow empirical testing (cf. Smith, 1991).

Why didn't farming happen before 10,000 BP?

If Winterhalder and Goland are correct it might well be asked why farming did not appear before 10,000 BP. If the broad diet characteristic of recent, low-latitude hunter-gatherer populations is so similar to that of chimpanzees it may have characterized the common ancestor of humans and chimpanzees, and therefore have an antiquity of up to seven million years. One of the most exciting aspects of the Winterhalder and Goland model is that it allows farming to be regarded as a special case within a wider range of possible adaptations.

Since the divergence of the evolutionary lines leading to chimpanzees and *Homo* there have been several periods when the world's climate has experienced a rapid increase in aridity which, in certain habitats, favoured the growth of grasses. Vrba identifies one such period at 18 thousand years BP and another at 2.5 million years BP (Mya). During the '2.5 Million Year Event' cooling initiated the spread of more arid and open environments in East Africa. Forests were displaced by grassland. There is good evidence for the effect of this event on the adaptive evolution of bovids, antelope and the grasses themselves. Similar changes appear to have occurred in South Africa, although it is not certain that they occurred at the same time (Vrba, 1988, pp. 407-8). Vrba regards the evolution of robust australopithecines (Paranthropines) as another adaptive response to this climatic change, arguing that the thickened tooth enamel, expansion of the posterior teeth, reduction of the anterior teeth and expansion of the masticatory muscles all point to an adaptation to the resources prevalent in an arid, open environment (Vrba, 1988, pp. 417-18). These adaptations may have occurred independently in South and East Africa, or robust forms which had evolved in South Africa may have colonized the East African grasslands. The hypothesis that the robust australopithecines adapted to a specialized

diet of hard, small and low-quality foods found in savanna environments is generally accepted (Bilsborough, 1992, p. 107; Foley, 1987, pp. 242-3; Grine, 1988), but is not beyond question. Grine notes that *Paranthropus* tooth-wear may be similar to that observed on chimpanzees (Grine, 1988, p. 515). Brown and Feibel argue that robust populations persisted in the Turkana Basin throughout the period between 2.5 and 1.4 Mya BP, despite several changes of climate (Brown and Feibel, 1988, p. 339; see also Bilsborough, this volume, pp. 53-8).

On the balance of probabilities, however, the evolution of the robust australopithecines offers some parallels with the appearance of cultivation among some modern human populations. The robust australopithecine/*Paranthropus* populations specialized in hard foods that might, arguably, have been situated at the base of, or even beyond, the optimal diet of the gracile forms and, later, early *Homo*. Just as cultivation sustains a greater population density than does hunting and gathering, so the robust *Australopithecus boisei* fossils outnumber those of the contemporary *Homo habilis* by 2 to 1 (Foley, 1987, pp. 242-3).

How often did this evolutionary trend take place? Wood (1988) assesses the evidence for the independent evolution of 'robust' features in different australopithecine populations. It is conventional to subsume three taxa into the 'robust' category: *Australopithecus (Paranthropus) robustus*, *A. (P) crassidens* and *A. (P) boisei*. While regarding the evidence that these three species were monophyletic as overwhelming, Wood notes that up to one-third of the robust characters may have been independently developed and that most of the characters linking the robust species are strongly related to a single functional (i.e. adaptive) complex, the masticatory system. They could therefore have evolved as a result of convergence between different populations adapting to similar ecological niches (Wood, 1988, p. 272). Others have argued more strongly for the view that there were several robust australopithecine lineages; and suggest that the adaptation which favoured the selection of robust features may have occurred independently two, three or even four times over a period of one to two million years (Foley, 1987, pp. 251-4 and this volume; Grine, 1988, pp. 511-12). The most tenuous of conclusions might be that such an adaptation occurred approximately once every half a million years; that is to say, at a rate equivalent to no more than one occurrence within the evolutionary life span of modern humans. I shall argue below that the Younger Dryas may have been the critical moment for such an adaptation to succeed.

What is the specific niche within which cultivation becomes a successful adaptation?

A simple increase in aridity is not sufficient to induce a hominid evolutionary trend toward the exploitation of seeds and roots. The evolution of human hunter-gatherer adaptations must, as argued by Foley (1987, p. 239ff), be seen in its ecological context. The robust australopithecines co-existed at first with *Homo habilis*, and later with *H. erectus*. They became extinct at about 0.9 Mya, at the time when representatives of *Homo erectus* migrated out of Africa. Any early member of the genus *Homo* who attempted to adapt to a lower grade diet would have faced competition from the already well-adapted *Paranthropus* populations. The robust australopithecines would themselves have faced competition from baboons and herbivores (Foley, 1987, pp. 223-4, 255).

Once out of Africa, and within Africa after the time of the robust australopithecines' extinction, neither *Homo erectus* nor *Homo sapiens* would have faced competition from their nearest evolutionary relatives. In Africa, however, baboons were still occupying a similar ecological niche. Both within and beyond Africa, large herbivores would have competed for grasses and pigs for roots. It is noteworthy that in central Australia, where there are no large native herbivores, grass seeds played an increasingly important part in the diet after 3500 BP (Cane, 1989; Smith, 1989). In the Kalahari, where large bovids are abundant, grass seeds are not part of contemporary hunter-gatherer diet (Lee, 1968). We do not know whether hunter-gatherers collected grass seeds in the Kalahari prior to the introduction of domesticated livestock to the region.

It now appears conclusive that it was the worldwide cooling of the earth's climate known as the Younger Dryas (c. 11,000-10,000 BP) which prompted the origins of agriculture in the Near East (McConiston and Hole, 1991; Moore and Hillman, 1992). This would have been the first such event since modern humans (following the dominant contemporary model) had spread out of Africa. Even within the Near East, however, there was a diversity of habitats and the cultivation of cereals was not the only response to this change in climate. In the southern end of the region occupied by the Natufians, people responded to increased aridity by abandoning their sedentary villages and reverting to nomadism (McConiston and Hole, 1991, p. 50). Even in the Natufian 'heartland' a brief period of nomadism preceded the first signs of cultivation (Moore and Hillman, 1992, p. 491). The case study of Aboriginal cereal husbandry in the Lake Eyre Basin of Australia outlined in Layton, Foley and Williams 1991, pp. 258-9) also

illustrates how finely balanced the alternative strategies of nomadism and sedentism may be. McConiston and Hole point out that the Younger Dryas climatic phase was distinguished by 'hyper-arid summers' which particularly favoured annual species of cereals and legumes in certain parts of the Near East (McConiston and Hole, 1991, p. 46).

The social organization of farming

Whatever parallels may be drawn between the adaptation of the robust Australopithecines and the strategies of the first cultivators, it is clear that the former cannot be described as farmers! What was the critical difference? It may be tempting to identify it in the technology used by early farmers, but I question whether this is the most significant difference. Ehrenberg has suggested that there might be a distant common phylogeny linking the chimpanzee termite probe to the human digging stick (Ehrenberg, 1989, p. 48) and it is by no means established that the earliest stone tools were associated with *Homo habilis* rather than the contemporary robust Australopithecines.

From the perspective of social anthropology, humans are distinguished by their uniquely complex social organization. This form of social organization provides the essential basis for the reciprocal and co-operative patterns of productive activity on which farming depends, the patterns which James Scott termed the 'moral economy of the peasant' (Scott, 1976, and see Panter-Brick, 1993, for a comparative discussion of these practices). Dunbar has recently argued that the evolution of the human capacity to construct social relationships can be tracked through the evolution of the neocortex. He argues there is a direct relationship between the size of the brain's neocortex and 'the number of relationships an animal can keep track of in a complex, continuously changing social world' (Dunbar, 1993, p. 681). Comparison of neocortex size and social group size among other primates leads to two predictions: that modern humans should be able to keep track of between about 150 and 250 relationships, and that this capacity has existed since modern human brain size was attained, about a quarter of a million years ago (see also Bintliff, this volume). Dunbar argues that both hunter-gatherer bands and Neolithic village communities in Mesopotamia were of about this size (Dunbar, 1993, p. 686). He proposes that language replaced grooming in the course of human evolution to enable group size to increase. Does acceptance of such a basis for the uniqueness of farming entail a retreat into progressive evolutionary models?

This would not be the case if it could be demonstrated that these

social skills evolved as a specific adaptation to hunting and gathering in certain environments. I consider that Dunbar is wrong to conclude that hunters and gatherers live in face-to-face communities of the critical size range he has identified. A comparison of group size among chimpanzees and hunter-gatherers shows that hunter-gatherers living in low latitudes behave in a similar way to chimpanzees with regard to the size and the fission-fusion pattern of foraging units, but differ markedly both in recruitment to the local group and in inter-group relationships. The typical hunter-gatherer band is no larger than the chimpanzee troop. Among chimpanzees, males are confined to the same local group all their lives. Females are able to change group membership only as young adults. Chimpanzee local groups defend the boundaries of their territories against other chimpanzees. Among hunter-gatherers such as the Mbuti and !Kung, adults of both sexes can change band membership freely, taking advantage of that larger set of relationships Dunbar has identified. Neighbouring bands frequently forage over each other's territories (see Ghiglieri, 1984, pp. 182-5 and Goodall, 1986, p.147 on chimpanzees; Turnbull, 1965, pp. 96, 220-1 on the Mbuti and Lee, 1979, pp. 42, 72 on the !Kung). Among the Mbuti, relatively little effort appears to be put into maintaining inter-band relationships but, among semi-desert hunter-gatherers such as the !Kung of the Kalahari and the Pintupi of central Australia, inter-band relationships are carefully maintained through the exchange of gifts (Wiessner, 1982; Myers, 1986, especially pp. 170-7). Both Wiessner and Myers argue that energy is invested in gift exchanges to reduce risk in an environment where resources are patchily distributed and unpredictable in their abundance. Turnbull, however, concludes that the Mbuti live in a fine-grained environment in which a band can expect to subsist throughout the year on resources within its own territory (Turnbull, 1965, pp. 149, 173). These observations suggest that the uniquely human pattern of social relationships which evolved among hunter-gatherers would have been most adaptive if it had evolved in an unpredictable savanna or semi-arid environment. It is in just such an environment that much of human evolutionary history took place (see Bilborough, this volume pp. 58, 71-4). The point has been made before that the earliest farmers of the Levant were heirs to a Natufian hunter-gatherer culture which had developed the storage of grain (e.g. McConiston and Hole, 1991, p. 46). I argue that it is not the development of delayed return social systems which is crucial, but the earlier development of the long-term investment in complex *social relationships* to be found even in so-called 'immediate return' hunter-gatherer societies.

Table 5.1: Foraging units, bands and regional communities

	foraging set	band	community	source
<i>Chimpanzee</i>	males: 4-5 females: 1-14	20-100	absent	Ghiglieri 1984 Goodall 1986
tropical forest:				
<i>Mbuti</i>	males: 1-2 females: 2-3 (net hunting: c. 30)	40-75	cf. <i>Aka</i>	Turnbull 1965
<i>N'Dele Aka</i>			500	Hewlett et al., 1982
<i>Batek De'</i>	men: 1-2 women: 2-3	20	200	Endicott 1979, 1988
tropical coast:				
<i>Gidjingali</i>	men: 1-3 women: 2-7	14-80	3-400	Jones 1980 Meehan 1982
tropical savanna:				
<i>Hadza</i>	men: 1 women: 2-10	3-37	50-150	Woodburn 1972
semi-desert:				
<i>Dobe !Kung</i>	males: 1-2 females: 2-4	10-120	145-460	Lee 1979 and <i>pers. comm.</i>
<i>G/wi</i>	men: 2 women: singly?	20-100		Silberbauer 1981
(except annual biltong hunts)				
<i>Yankunyjatjajara</i>	males: 1-2 females: 1-10	c. 35	250-600	Layton 1986

Sources: Endicott, 1979, 1988; Ghiglieri, 1984; Goodall, 1986; Hewlett et al., 1982; Jones, 1980; Layton, 1986; Lee, 1979 and *personal communication*; Meehan, 1982; Silberbauer, 1981; Turnbull, 1965; Woodburn, 1972.

Conclusions

If farming looks like an unique evolutionary 'step forward' this is, then, due to a particular coincidence of circumstances. This chapter has considered evidence for biological mechanisms which tend to stabilize hunter-gatherer population levels, and proposed that similar constraints would have applied to the gracile Australopithecines. The paper has further argued that particular, contingent changes in climate and ecology may have the effect of destabilizing these processes, leading to the evolutionary divergence of populations pursuing alternative strategies. In this regard, the robust Australopithecines are argued to have adopted a dietary strategy similar to

that of early farmers, namely a concentration on low-ranking plant foods such as seeds and roots. This contribution has concluded that sedentism may have a different effect to nomadism on the physiological mechanisms that control human ovulation rates, allowing population levels to increase. The relatively greater number of robust Australopithecine fossils suggests that their presumed diet may, for a long time, have enabled a more successful adaptive strategy than that of the early hominids who persisted with broad-based omnivory. In appropriate environments, cultivation may also confer a similar evolutionary advantage over hunting and gathering. It has also been argued that the type of sedentism characteristic of the early farmers does not depend on a unique form of social organization but rather provides a new context for the expression of uniquely human capacities for constructing complex social relationships which had evolved with the appearance of modern humans and already had some antiquity by 10,000 BP. Finally, the frequency with which related species had, in the more distant past, adapted to similar ecological circumstances suggests that the appropriate niche for the specialized exploitation of wild grasses and roots may only appear infrequently, and may not previously have arisen since the appearance of modern humans. The appearance of farming about 10,000 years ago is thus argued to be the consequence of a chance coincidence of events, in which a species with novel forms of behaviour first encounters a rare climatic event.

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6 History, ecology, contingency, sustainability

I. G. Simmons

Summary

Changes in the ideas fundamental to ecological science are discussed and applied to models of archaeology and history which claim to possess similar interactive and dynamic characteristics. Examples such as domestication of plants and animals and industrialization appear to belong to the class of self-organizing dissipative structures for which prediction is unlikely. In a wider context, this seems as if concepts like sustainability belong to equilibrium worlds which do not exist. Historical disciplines which seeks to place themselves in the framework of the 'Green Debate' will need to be aware of these wider epistemological considerations.

Humanity and environment, past and present

One of the great concerns in the world today is that of the relation of the human population to its non-human surroundings. From the local scale of waste tips near backyards to the possibilities of accelerated global warming, 'the environment' is coming under scrutiny as never before. After this interrogation of nature, societies are asking themselves rather searching questions about our role in the perceived disharmonies and potential catastrophes. The past is being scoured for any lessons that might contribute to the solution of present problems: Pleistocene ice ages and Dickensian ice-fairs

alike are investigated for general messages for humanity and, more pointedly, our social structures.

Between the Cromerian interglacial and the wrong sort of snow on commuter railways comes the contribution of archaeology, with some emphasis on the earlier part of the period. In general, archaeology, though by no means confined to 'pre-literacy', has not looked onwards to link with its junior cousin, history, in providing a commentary on human-environment relations in the past, as a context (and maybe a perspective) for today's concerns. In the volume *All Natural Things: Archaeology and the Green Debate* (Macinnes and Whickham-Jones, 1993), the only attempt at such a long view is in fact written by a geographer, though that chapter (Coones, 1993) deliberately concentrates on landscape rather than environment.

Human cultures can constru(ct) 'the environment' in various ways (Simmons, 1993a) but for archaeologists two of them are predominant. The first of these is environmental archaeology, which uses a battery of positivist-based techniques that feed into an epistemological framework which is usually ecological, for it claims to be a discourse about the dynamic interaction of humans, their societies and their surroundings. The second is predominantly cultural, in which environment is a mental construct and 'nature' is a production of social knowledge, mutating as the foci of that knowledge alter (Fitzsimmons, 1989; Tilley, 1990). In this essay, the emphasis will be upon the ecological rather than the uniquely social in the sense that it will be based upon the notion of a critical realism, but using the ecological in a manner more theoretical than empirical. This helps to bridge the gap between it and the social world. It is thus in contrast to much science-based writing on 'green' issues, which assumes that the natural sciences provide 'facts' to which the rest of society must then adapt. In the present context, science is largely responsible for providing the historic data which underpin explanations of the sequence and timing of causal events in archaeology and environment (Winterhalder, 1993).

The discipline of history has come to engage with the human environment more recently than archaeology, as well as dealing with the more recent past. Forsaking earlier simplicities of the deterministic kind, environmental history is now established as a field in which the influence of environment on culture and vice-versa is seen as mediated through the full spectrum of human behaviour (Simmons, 1993b). There are still different kinds of historiography, even of the environmental kind. Attempts may be made to recover the fullness of the past exactly as it happened, following the epistemological mode of the natural sciences, or to

discover that there has been progress towards the better state of today (or in the case of environment, often worse), and to construct national identity through resource use and landscape patterns (Applebey et al., 1994). In these studies, the terrain and the document are the primary sources (see for example Grove, 1995): the mingling of say palaeoecological and documentary data at anything other than the local scale is still uncommon though increasing.

Ecological theory

In any reconstruction of past environments, the science of ecology very probably will be invoked. In contrast to several of the contributions to this volume, its time-scale covers approximately the last 10,000 years rather than the last 10 million (or whatever) of evolutionary time. This may result in a different balance of the predictable and the contingent (as outlined by S. J. Gould in his Introduction), for the generalities which give rise to the predictables are likely to be overshadowed by the contingencies of detail in a world which humans have made both materially and symbolically. Given, indeed, the human capacity both to construe and construct worlds, we need to think about whether reflexive cultures are more likely to increase predictability or contingency, assuming we can measure either. Add to this the scientific view that at no time in the Holocene have climates been so stable that ecosystems could come into some kind of equilibrium with them, and we have a recipe for a restless world. Ecological science, however, has in general lacked an accepted body of theory by which to order these data (MacIntosh, 1980). This is characteristic of many historic sciences (like palaeontology, geology and evolutionary biology) when compared with fields like physics, chemistry and molecular biology where there is little reference to the history of the system (Peters, 1991).

Equilibrium models

Nevertheless, one of the most pursued ideas in the science of ecology has been the search for equilibrium as part of its project of imposing order upon nature (Kingsland, 1985). Its emergence in the 1930s, from being concerned largely with spatial catalogues, was hence marked by a quest for equilibrium, harmony and order. The ideas of luminaries such as Paul Sears and Aldo Leopold were gathered up by Eugene Odum (1969) into a view of nature as a series of balanced ecosystems which followed a strategic pathway towards maturity, an end-point equated with the concept of

'climatic climax'. (The steady-state is like the notion of a no-growth economy and in fact the latter is much influenced by ecological concepts of stasis.) The mature state is one of high species diversity, stable biomass and close nutrient cycling. This is evident in the many examples of succession given in ecology texts, where bare rocks recently emerged from under Pleistocene ice become successively colonized by plants of greater size and complexity, building up to an inevitable mixed forest, in equilibrium with the climate prevailing just before humans felled the trees. In the same way, open-water kettle-holes gradually fill up and become indistinguishable parts of the forest landscape.

The same models could be adopted where human presence caused disturbance of the vegetation. The observation of swidden agriculture in the tropics emplaced a model of the recovery of forest once a clearing had been abandoned. First shrubs, then light-demanding trees and finally the shade-intolerant 'climax' species, filled the gap; eventually the forest regained its original physiognomy and species composition. Such models pervaded environmental archaeology through the palaeoecologists' treatment of the pollen-analytical evidence for Neolithic (and, later, other periods') land-clearing for agriculture, especially the accepted archetype of the *landnam* colonization and abandonment as proposed by Iversen (1941). Many palynological investigations have subsequently described the post-cereal phases in terms of a linear succession of herbaceous plants and ferns, shrubs, small tree species and finally the components of the climax forest.

Non-equilibrium states

Within an overarching intellectual structure much influenced by the discoveries of quantum mechanics and the notions of both self-organizing and energy-dissipative structures (Prigogine and Stengers, 1984), ecology has more recently abandoned equilibrium, harmony and order for studies of disturbance, disharmony and chaos (Worster, 1993). The challenge to older modes of thought is often dated to a paper by W. H. Drury and I. Nisbet (1973), with amplifications through the later 1970s. Work from the north east woodlands of the USA suggested that succession did not necessarily lead anywhere, least of all to a stable, fully replaced climax forest. There certainly was change following the creation of openings but it was without a determinable direction and never reached a point of stability. The forest was therefore to be seen as an erratic and shifting mosaic of trees and other plants. Detailed studies of both past and present confirmed that disturbance was

common in nature from fire, senescence and windthrow, and so by 1985, Pickett and White could describe virtually all naturally occurring and human-disturbed ecosystems as mosaics of environmental conditions: a landscape of patches.

The theorization of this type of empirical work was pioneered by R. M. May, whose simplest formulations (1976) followed those of the emerging field of *Chaos Theory*, which is based on simple mathematical models with very complicated dynamics. Chaotic systems have a very sensitive dependence upon initial conditions, with the difference between trajectories growing exponentially through time. Thus, some predictions can be made over short time periods but over longer periods they are not possible because the trajectories move apart. Yet large-scale structures can passively contain what happens at smaller scales even if they are not simply the mechanistic results of what happens below. Causality in ecosystems is not therefore easily understood by strict reductionism. It is no surprise therefore to see gaps in approaches to theory. On the one hand there have been field-oriented ecologists whose interaction with theory was mostly confined to data processing and computer simulation. The resulting regularities might be taken as representing law-like behaviour, as in e.g. Lawton (1989). On the other hand, primary theoreticians used techniques of mathematical analysis and the derivation of equations in abstract models of systems (often idealized) or parts of systems, as in Hassel and Anderson (1989).

So it was only in 1988 that Hall demonstrated that many of the prominent models in ecology that underlay a great deal of what had been used as a theoretical (and in fact pragmatic) base was deficient in data and validation and often had a colourful sociological history. The logistic curve and its derivative the Ricker curve (often used as a management tool in fisheries), and Lotka-Volterra predator-prey relationships are quoted as examples. Hall expresses no surprise that the relationships portrayed in these models do not function simply, since he notes that even a basic tenet of physics like Ohm's Law does not work at very high nor very low voltages, where non-linearities prevail. Pimm et al. (1991) show that even the most simple models of population change in natural ecosystems show a variety of behaviour that includes a simple return to equilibrium, but also cycles, cycles on cycles, and chaos. Any ecosystem subject to human actions might be even more complex or, under the influence of a unitary worldview and a massive technology, drastically singular.

The current outcome of these findings is that chance and contingency are likely to play a strong role in the outcomes of any

set of processes within self-organizing systems. The butterfly effect may well work, but nobody seeing the fluttering in Tokyo knows that the storm will be in New York. For any archaeology that is interested in contributing to the history of the relations of human societies and their environments then the first question, 'Is nature predictable?' receives the answer, 'By and large, no'. The second question must then be, 'Does the possession of all that we call culture make human societies more or less open to chance and unpredictability?'

Sustainability, past and present

There are two main reasons why we might be interested in these questions. The first is the more-or-less purely academic one (and none the worse for that) of wondering whether the great changes in the human-nature relationship were in any sense inevitable in time and place: were the discoveries and processes that led to the adoption of domestication bound to happen, driven by a particular set of circumstances or is what we now see just the few remaining unpruned branches of a once more prolifically radiating tree? Why industrialization in Europe in the eighteenth and nineteenth centuries and not in China? The second is more pragmatic in nature. It revolves round the current shibboleth of 'sustainability'. Nowhere is it possible to move in the field of environment studies, even in the Stationery Office catalogue, without seeing this concept, elevated to the standing of the Golden Calf at the 1992 Rio de Janeiro 'Earth Summit'. It seems to be regarded as some kind of teleological omega-point when combined with the words 'development', 'use' or 'economy'. So students of the past might reasonably be asked questions about SEs of historical and archaeological times: were there sustainable economies and did they last? And to what contingencies were they subject in both their arising and their breakdown? After all, in 9000 BC, hunting and gathering might have been judged to be a sustainable economic mode but in 2000 years it had disappeared from most regions except those now deemed to be marginal to agriculture and pastoralism.

The question of the adoption of domesticated animals and plants as the foundation for an economy, is discussed in Chapter 5 of this volume by Robert Layton, who provides evidence that the transition is not irreversible. He suggests that people move fluidly between social bands in a context where one band may be cultivators and another hunters. Another source of variation is the rate at which crop plants might become domesticated: Hillman and

Davies (1990) allow this to be as little as 20–30 years if a cereal crop is harvested at near-ripe stage by sickle-reaping or uprooting, and if it is sown on virgin land every year. Crops harvested when much less ripe complete the same process within 200 years. In the present context, the point is that such rapid transitions are likely to be archaeologically invisible and so many of the failed transitions or the deliberately reversed passages remain undetected.

Something similar may be true of the adoption of cultivation as well as its early emergence. Pollen-analytical studies at North Gill on the North York Moors (NE England), using counts every 1 mm vertical interval, have revealed a phase of some interest (Turner et al., 1993; Simmons and Innes, 1996). Its dating is not simple since the 14C dates in the profile are not sequential, but the most likely time is *c.* 4700 cal BC, which is a typically early Neolithic date. The pollen diagram is given in full in Simmons and Innes (1996) and a simplified abstraction from it appears as Figure 6.1. The phenomena of greatest interest are described below.

An abrupt change in some pollen frequencies at 747 mm signals the beginning of the disturbance phase. Total tree pollen (AP) falls and is replaced with hazel (*Corylus avellana*). Within the trees, *Quercus* (oak) and *Tilia* (lime) fall whereas birch and pine increase, as does, temporarily, elm. Alder (*Alnus*) displays no sudden response but begins a gradual and sustained rise. Grasses are generally low in this phase but the *Calluna* (heather) curve rises suddenly, as does bracken though its levels are never very high in this profile. A number of herb types typical of open ground manifest themselves either for the first time or after a long interval: *Epilobium*, *Silene*, *Artemisia*, *Taraxacum* type and *Cruciferae*. But the outstanding feature is the sudden and sustained presence of *Melampyrum* (cow-wheat). Immediately after an initial peak, it declines swiftly (and indeed is absent at 743 mm) but rises again to levels of almost 20 per cent (of AP + other herbs) before falling sharply to much lower levels as soon as the first cereal grain is detected at 725 mm. Both Macroscopic (MA) and Microscopic (MI) charcoal are present throughout the phase with peaks coinciding with those of *Melampyrum*. There are 21 samples in the phase, which suggests a length of 131 years.

The cereal grains are all found within the phase 718–725 mm. Eight samples at 6.25 yr/sample suggest an episode of 50 years. Birch declines suddenly half way through this phase but is mirrored by the oak curve. Pine falls irregularly and is almost absent by the end of the phase. Elm, lime and alder seem little affected, though perhaps all benefit slightly, as does ash; a few grains of *Fagus sylvatica* (beech) are found. Hazel is irregular but exhibits no

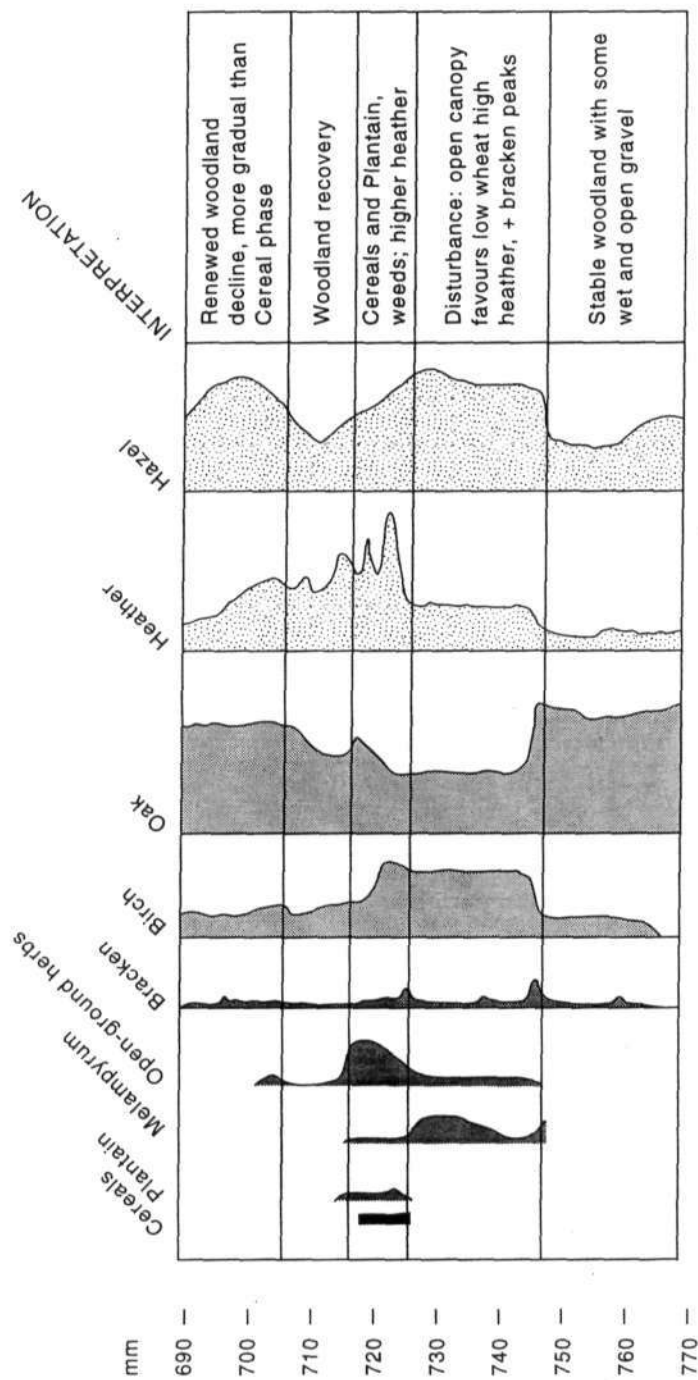


Figure 6.1 Analytical pollen studies at North Gill, North Yorkshire. Based on Simmons and Innes (1996)

great surge; willow falls dramatically to zero before a small peak; *Prunus* and *Crataegus* (small trees and shrubs of scrubby fringes) increase a little. There is a high peak in heather and grasses are somewhat raised in frequency compared with the preceding subzone, though lower than at the base of the profile. *Pteridium* (bracken fern) is distinctly higher though not at very high frequencies. Sporadic herbs make a distinct pattern of increased presence after being mostly absent and include *Scrophulariaceae*, *Cruciferae*, *Chenopodiaceae*, *Genista*, *Anagallis arvensis*, *Polygonum aviculare*, *Senecio* type, *Taraxacum* type, *Artemisia*, *Cirsium* type and *Matricaria* type. These are herbs associated with broken ground such as arable fields. A dramatic change comparable to the onset of *Melampyrum* in the preceding phase is its demise to very low levels as soon as the cereals appear, with its place being taken, as it were, by a plantain (*Plantago lanceolata*) curve which itself lasts only as long as the cereals themselves. MI charcoal shows a moderate peak during the time of the cereals but there are only three, spaced, occurrences of Macroscopic charcoal, only one of which is at a cereal grain horizon.

The length of the fire-maintained *Melampyrum* phase (130 years) is entirely comparable to some of the other North Gill phases with a similar ecology. The shift in intensity of management which marks its beginning appears to be greater than that which indicates the cereal-*Plantago* phase. This allows the inference that the cereal growing was slipped into a patch of land which had hitherto been used for another purpose but whose usage had not robbed it of its suitability for arable cultivation (Simmons and Innes, 1987). In this instance, the abandonment of the area after 50 years and the absence of similar instances elsewhere in the immediate vicinity of the North Gill bring about the inference that this was an optional food rather than the vital item of subsistence that it was later to become. In other words, here is a chance trial of a new food that led nowhere. In the circumstances of relatively low levels of manipulation of the vegetation, any view of a minimum population size for sustained agriculture looks apposite.

Such contingencies notwithstanding, settled agriculture did become the dominant *genre-de-vie* in North Yorkshire, and in rather a lot of other places as well, most of which have stayed that way for a long time. This part of upland Britain has slipped between agricultural and pastoral use several times, each change being driven by external economic circumstances of which, unsurprisingly, industrialization is and has been one. Is there a parallel set of circumstances in which there was movement in and out of this new phase before it became dominant? An outstanding attempt at an

ecological interpretation of the emergence of industrial economies into the early modern (in European terms) is that of E. L. Jones (1981), whose view of environment is that it imparts a direction but does not give precise marching orders. Likewise, he discovers no overarching theory with a social basis for the rise of Europe and not Asia to industrialism; indeed he thinks that in Europe the various risks posed to society were lower than in Asia and that the 'options were simply a little broader'. Within that framework, Jones concludes, long-term economic change was much more than the usual conception of an economic process. He adds that factors such as personal security, predictability of government actions and a reliable currency are likely to have been important elements. The concatenation of all of these seems prone to chance occurrences (see also Bintliff, this volume). In that setting, events like Abraham Darby's move to smelting iron ore with coke (at Coalbrookdale in Shropshire in the eighteenth century) appear even more stochastic, even if they were (and this is often disputed) driven by shortages of wood fuel. Though many of the same preconditions were apparently present in Asia, the processes leading to the development and spread of industry as we know it did not flourish. Indeed, Gellner (1988) emphasizes the European social conditions to the exclusion of all else, suggesting that the values of Protestantism (order, an even spread of sacredness, and the idea that prosperity signified divine approval and eventual Election) provided the right seedbed for the germination of an industrialism which depended upon capital accumulation. The difference in discourse between these two explanations suggests even more strongly the existence of contingent factors.

Contingency and organization

Does, then, the possession of all that we call culture make the actions of human societies more or less open to chance and unpredictability? From the studies glanced at above, the answer seems to be 'they are still open to contingency, because they respond to some synergistic interactions'. In which statement there is an immediate echo of the type of change postulated by Prigogine and Stengers (1984) and mentioned above. Here, all systems contain sub-systems which continually fluctuate. At one point a single fluctuation or a combination of them will allow a leap into a new, more differentiated higher level of organization not predictable in the pre-existing situation. The new levels may also be called dissipative structures because they require energy to sustain them, and the higher the complexity of organization, the higher the input

of energy needed. Note also that the leap may be downwards into a unordered 'system', for which the ordinary-language terms would be 'chaos' or 'anarchy', and that the higher the input of energy the greater the production of entropy. This is virtually a 'collapse' of the type suffered by ancient Rome, warring states China and the Mayan cities. But as Tainter (1988) notes, nations nowadays can no longer collapse, being bound into a world-system.

Thinking of how the past has been affected by chance and how poor our prediction of the future is likely to prove (Treumann, 1991), it is unlikely that we can tell when and at what scale the swing of fluctuations is going to throw up a new dissipative structure (May, 1989; Forman, 1995). The evolution of agriculture and industrialism were clearly new dissipative structures in their time (consider for example their energy relations, detailed in Simmons, 1996), and were not predictable. Sustainability, on the other hand, derives in some usages from an equilibrium concept of system behaviour: carrying capacity is often invoked. In so far as few systems seem to be in equilibrium (and some economists have now moved radically towards a much more ecological view of the world: see for example Barbier [1993]), this view of sustainability is of a doomed enterprise. By contrast, if sustainability is capable of being pragmatically and epistemologically self-organizing, it may well become an ingredient of a new set of dissipative structures. But the time-span of any sustainable economy is likely to be a finite episode rather than an omega-point teleology (McGlade, 1995). The paradox is, of course, that most new structures that ecologically minded environmentalists contemplate are those which produce far less entropy (Georgescu-Roegen, 1982). Whether, indeed, the term 'self-organizing' can be equally applied to chemical, biological and social systems is debatable (Mingers, 1992; Swenson, 1992). In more everyday terms, classical economic and social variables provide signals which are then converted to actions which are likely to be highly dependent upon local and particular circumstances, i.e. contingent (Rapport, 1991). In this contingent, regional, discursive and democratic setting, some see the best way out of current social problems with an environmental delivery route (Hayward, 1994).

The lesson for archaeologists and historians (and us lesser breeds) who are minded to take an interest in the fluctuations of time, nature and humanity, seems to be that change is unpredictable and contingent but has so far been towards the creation of dissipative structures producing ever higher amounts of entropy from the oxidation of fossil fuels to the loss of species. Environmentalists say that a stasis or even a reversal must take place; my money would be

on some set of structures we have not dreamed of and the raw materials of which come from humans and not from nature (cf. the discussion in Redclift, 1993.) This means that the present, like the past, is one of radical uncertainty: environmentalist Utopias are subject to the same problems as all the others. One of the texts of the Talmud says that there were 26 previous attempts to create the Universe and all of them failed. God accompanied the most recent attempt with the words, 'Let's hope it works'. Amen to that.

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7 Structure, contingency, narrative and timelessness

John Bintliff

Summary

This chapter will analyse the dynamic morphology and evolutionary history of three familiar animals from historic times: *Polis micra*, *Villa Romana* and *Ecclesia parva*. Stephen Jay Gould's concepts of punctuated equilibrium and historical contingency, together with Le Roy Ladurie's model of 'timeless history' will be employed to interpret the evolutionary history of these two fossil and one endangered species

Introduction

In a presidential address to the American Historical Association, published in 1979 and entitled 'The Renaissance and the Drama of Western History', William Bouwsma drew attention to a recent and remarkable event: the collapse of the traditional dramatic narrative organization of Western history. That old dramatic pattern relied on a concept of linear history moving the human race undeviatingly to its goal in the modern world. The trinity of acts composing the great drama of human history – ancient, mediaeval and modern – saw the modern era as the last act and allowed the Renaissance to be

privileged as a critical transition period to the present world. The downfall of this approach can be attributed to a convergence of factors: firstly, the growing disbelief that any era, including the present, can emerge through some kind of single linear process, instead of being a complex product of a tangled past; secondly, and even more powerfully, the collapse of the idea of progress as an organizing principle for history; and thirdly, the important critique that has emanated in recent decades from social history. That very significant subdiscipline has shifted historians' focus to the neglected and suffering majority of humankind and diverted attention from those elites whose achievements have been the mainstay of claims for the special evolutionary status of periods such as the Renaissance. These pressures have left the Renaissance in partial eclipse.

A striking, iconoclastic example of rethinking the narrative of Western history, and highly influential on Bouwsma's paper, appears in an article in the journal *Annales* by the French historian Le Roy Ladurie (1974, reprinted in English in 1977). Ladurie offers a general interpretation of the extended period between the fourteenth and the eighteenth centuries of our era in Western Europe. Situated between two eras of innovation and expansion, this age is given essentially negative characteristics as an era typified by a grim Malthusian balance. The productivity of agriculture was limited, population was limited by that and by the recurrence of plague and persistence of disease, and the material conditions of life for the vast majority were virtually unchangeable, as was their exclusion from the elite superstructure of the powerful. By the democratic criteria of population numbers¹ and average lifestyle, this long period was changeless except for insignificant detail. Ladurie's paper is accordingly entitled 'Motionless history'. And to counter obvious reactions, Ladurie writes:

One might object to this conception of motionless history ... because it is a little too negligent of such fundamental innovations of the period as Pascal's divine revelation, Papin's steam engine and the growth of a very great city like Paris, or the progress of civility among the upper classes as symbolized by the introduction of the dinner fork. ... But what interests me is the *becoming*, or rather the *non-becoming* of the faceless mass of people. The accomplishments of the elite are situated on a higher and more isolated plane and are not really significant except from the point of view of a noisy minority, carriers of progress without doubt, but as yet incapable of mobilizing the enormous mass of rural humanity enmeshed in its Ricardian feedback (Ladurie, 1977, pp. 133-4).

From this standpoint the Renaissance appears as little more than an early aspect of this long, directionless era or *conjuncture*, and Bouwsma comments:

One has only to substitute ... any random set of Renaissance accomplishments – Petrarch's historical consciousness, the Copernican Revolution, the Florentine city-state with its civic rhetoric, and double-entry bookkeeping, for example – to appreciate the mordant implications here for the Renaissance (Bouwsma 1979, p. 7).

Bouwsma goes on to challenge Ladorie in turn to account for the 'avalanche' of forces that led to radical change from such a structure to the next, raising the problem of process left vacant with the demise of the model of linear progress. If Ladorie is correct, then change is cataclysm and the modern world is only remotely related to the past. Our own time is like a biological mutation whose survival value is an open question. For both Ladorie and Bouwsma, the era of timeless history to be sure accumulates innovations, but when at last the structure breaks and is transformed into the modern era, with the loosening of constraints on agriculture, the breaking of the old Malthusian cycle and the accelerated migration from field to factory, this cannot be conceived as an irresistible force rising over preceding centuries; the real explanation lies in contingency, and history is about suspense – the awareness that the drama might have turned out otherwise.

It must now be clear, that Stephen Jay Gould's philosophy of evolution (cf. Gould, 1990, 1991), as a form of history marked by a structure of punctuated equilibrium, finds many resonances in recent theory within the discipline of history itself: for both animal and human communities there are structures, periods of surface variety but little underlying change, whilst the succession of structures or eras that characterize both human and animal evolution are driven more by arbitrary and contingent factors than any inbuilt sense of direction and progress.

Both the earlier linear progress model and this newer punctuated equilibrium model are narratives that make the world comprehensible to us. The central importance of narratives to human perception can be shown through recent research on child development (Tucker, 1993). From fifteen months infants can role-play, answering for their dumb toys in imaginary conversations, and children rapidly learn how to capture attention by recounting mini-narratives. Such abilities probably lay the basis for later skills in understanding other people's wants and feelings, and enable the child to comprehend themselves and others through stories. Infants experience stability through reality-based play and fiction in which the children's own worlds are mapped and things are seen as they normally turn out; but they also experience challenge when games and stories offer a glimpse of a very different universe where events are unexpected, magical and arbitrary.

Playing with fear allows children to control moments of anxiety better in later life. A rather apposite example of our ability to cast our own lives into a suitable narrative can be found in a recent volume of *Current Anthropology*, where Richard Bradley interviews one of the founding fathers of archaeological theory in Britain (Bradley, 1993): the life story that unfolds through the interview is a confident tale of linear progress and directionality.

Development section

I would now like to explore briefly three specific applications of Structure–Contingency theory to historical archaeology.

The Greek polis (city-state)

Over a period of a few centuries in Iron Age Greece there arose a dense carpet of tiny city-states or *poleis*. The 'normal' polis on detailed study has an average total population of 2000–4000 (Ruschenbusch, 1985), not by chance large enough to be virtually endogamous and hence control all its lands. Forty years ago Ernst Kirsten demonstrated that the astonishing abundance of these tiny states is largely explained by revealing their true settlement status as large villages (Kirsten 1956; cf. Bintliff, 1994). The network of mature villages from which the cities emerge (the *Dorfstaat* as Kirsten termed it) betrays cross-cultural regularity in its modal territory of some half-hour radius of land. Over time the more powerful villages expanded their authority over neighbours, and many once independent villages and small cities became subordinate to a minority of dominant *poleis* (creating an average city-state territorial radius of an hour). With pressure to make the land more productive, a minority of citizens moved out to live in farms and villas outside the city. Thus by c. 500 BC there was established through most of southern Greece a 'structure' of village-towns within natural territories, often focused on larger cities and at the same time having their own satellite rural sites. This general pattern will persist without serious modification for some 1100 years until the late sixth century AD. To be sure the towns will grow and shrink, the farms and villas multiply and decrease, yet the structure of life remains little altered.

But the structural timelessness goes deeper than mere settlement pattern, into the socio-political sphere. In a number of recent papers the anthropologist Robin Dunbar (1992a,b) has argued that unstratified human communities will tend to adapt to our biological limits of not being able to process social relationships with more

than some 200 individuals. If a village does not fission at this point but grows far larger, it is because it has overcome this face-to-face organization through horizontal or vertical subdivision of the community. In the case of our typical Greek polis we find (Figure 7.1) that the normal form of government limited power to the nobles and wealthier farming class, some 200–400 or so adult males. Since only a certain proportion of these men would have regularly participated in the political process, it can be claimed that a vertical power hierarchy was well adapted to biological constraints. And once again we find that the power structure of the Greek landscape for some 1100 years remained one where characteristically an elite minority controlled the cities and their landscapes.

If we find here a structure with an underlying timelessness reminiscent of Ladurie, we may surely expect to find it in very different places and times. Indeed a similar structure recurs as a central focus of interest to historians of mediaeval Western Europe researching into the origin and development of the village community. During the late first millennium and early second millennium AD there emerged a widespread trend towards nucleated villages organized as 'corporate communities' by village councils with wide-ranging powers.² In 1086 for example, English villages were typically still at the face-to-face level of 150 people or less (Hallam, 1981), but population growth in the following three centuries could be accommodated through the crystallization of communal power around a minority of adult male yeoman farmers. The territorial scale of these expanding villages is commonly some half-hour radius. But although these corporate communities may have been responsible across wide swathes of Western Europe for the restructuring of land use into the two- and three-field system,³ they did not, at the village scale, transform themselves into city-states of the *Dorfstaat* type or develop an artistic and intellectual life in any way comparable to the Greek normal polis. For here historical contingency cuts through structural tendencies.

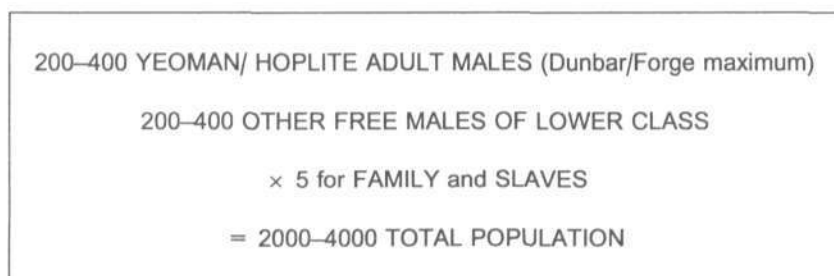


Figure 7.1 The corporate community: 'normal polis'

Archaic Greece with its proliferating village-states constituted a power vacuum, lacking significant dominant states and still beyond the reach of external colossi such as the Persian Empire; this chance circumstance opened up an almost unique dimension to the otherwise familiar process of population growth following a preceding cultural collapse (in this case the fall of Bronze Age palace civilization). The development of a landscape of corporate village communities might have been predicted, but the contingent absence of any superstructure of power freed the villages to assume total authority over their small worlds, to invent the state in the compass of a large English parish, with all the cultural impetus that such autonomy brought.

In complete contrast, the corporate villages of mediaeval Western Europe were almost entirely created under the watchful eyes of powerful states and their feudal lordship; real and important though the village councils were for land management and everyday law, there were always clear limits to freedom of action and investment of surplus wealth and labour. Only in Italy, where feudal powers were weaker and divided, can we see a mushrooming of city-states (between 200 and 300 by the twelfth century AD).

The villa in Roman Britain

My second case study looks at first sight ready-made for comparison with the evolution of biological species: the Roman villa in Britain. In the classic scheme of Collingwood and Richmond (1969) a linear evolutionary process encouraged the simple 'cottage' villa to unfold progressively into corridors, aisled and multi-courted mansions and palaces, through time, across the early to late Empire (Figure 7.2). In reality (Millett, 1990) early villas include several very large examples, and the trend over time is actually towards smaller complexes on average. It can be argued, therefore, that from the first the full range of villas could be found across the Romanizing landscape. However, Millett has pointed to an extension down the social scale over time of the desire and ability to live on a villa, so that much of the continuous rise in villa numbers to the fourth century AD, plus the lowering of average size, is accountable to the adoption by the lesser native aristocracy of the Roman country-house model. Remove the downmarket spread of villa construction and we find that the Collingwood/Richmond evolutionary trend is still perceptible for many long-lived villas, according to Percival (1987) and Scott (1993a,b). Is there therefore still some directional evolutionary dynamic in these morphological transformations?

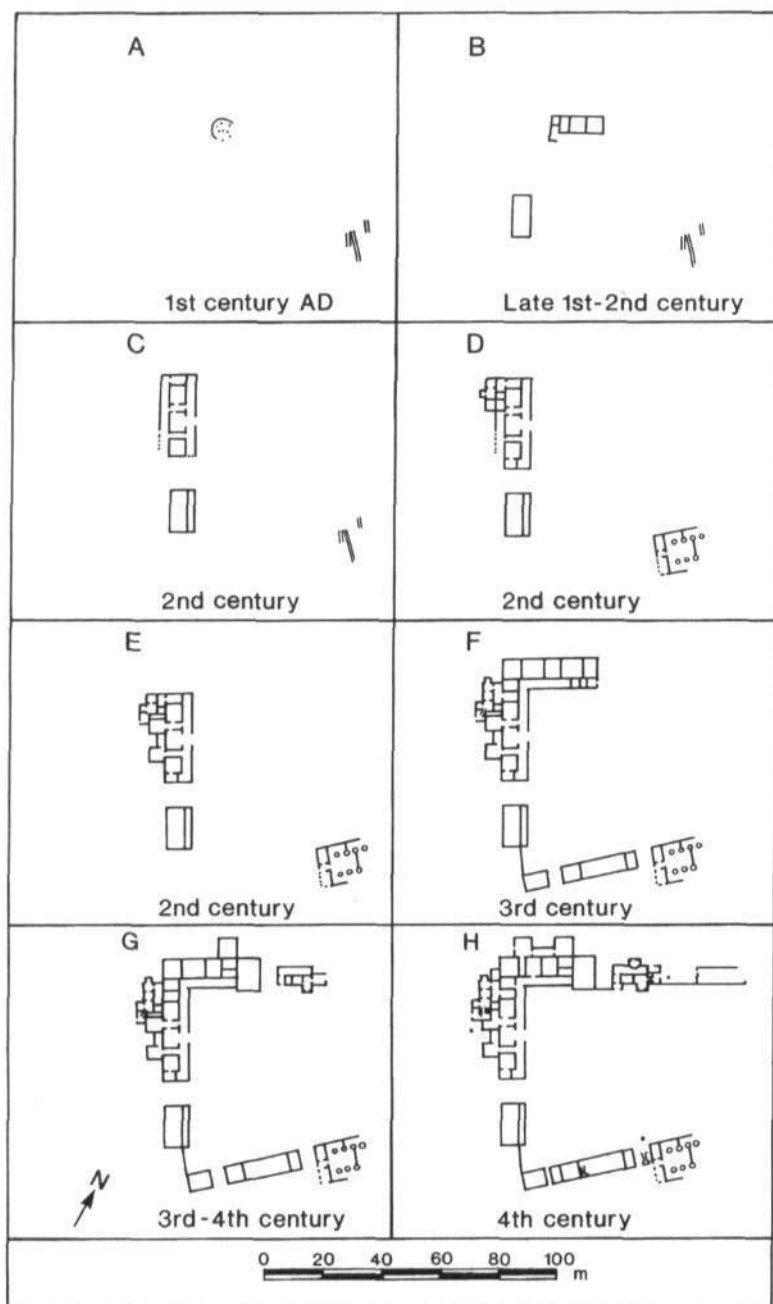


Figure 7.2 The development of the courtyard villa at Rockbourne, Hants (after Millett, 1990, fig. 79)

The answer, once more, seems to be no. In fact we can make a case that the whole sequence belongs to a much longer period of almost timeless structure of the Ladorie variety.

It is now widely claimed that villa-owners were usually native aristocrats; the multiplication of villas over time merely records the extension of Roman elite lifestyles amongst this pre-existing social stratum, both geographically and from the upper to the lower native landowning elite. The establishment, likewise, of a network of Roman towns across lowland Britain largely represents the Romanization of pre-existing native central-place systems (Cunliffe, 1991). Let me simplify the surface form of Roman Britain into its underlying structure: this is a society dominated by a landowning elite which operates in two arenas: (1) a regular network of regional central places (large and small towns) suitable for exercise of their power and responsibility, and for marketing the products of their estates, and (2) rural estate centres, the villas. Power and wealth rest within this minority stratum of Roman Britain, and the vast majority of the population remain in unpretentious rural farms and villages of pre-Roman plan and lifestyle.

This underlying structure developed in the mature pre-Roman Iron Age. According to Cunliffe and others (Cunliffe 1991; cf. Bintliff 1984), population rose dramatically through the middle to late first millennium BC. Power and wealth gravitated into the firm control of tribal aristocracies, whose activities are recognizable at two spatial levels: the lowland landscape became dominated by a network of regional and district central-places (the hillforts and later oppida) and amidst a plethora of lesser settlements a regular series of more pretentious estate centres (cf. Gussage All Saints, Tollard Royal, Thetford) are found in the countryside.

Could we not object that Romanization transformed native society through the appearance of true urbanism, or that heightened market conditions associated with incorporation into the Empire must have had a profound impact on population and production levels? If Roman urban population was a mere 6.5 per cent as Martin Millett (*op. cit.*) suggests, town life was hardly a radical new force disruptive of the role played by native central-places. The total population of Roman Britain, on admittedly limited data, seems as yet to show no dramatic fluctuations from the first to mid-fourth century, and the current consensus amongst both Roman and Iron Age researchers is that the high density of population was essentially achieved during the late pre-Roman Iron Age, before the Conquest.

The only remaining element susceptible to a linear, evolutionary approach would seem to be the evidence for villa enlargement and

elaboration over time. But here indeed much of what we observe is now argued to be a reflection of the reorganization of social space rather than the creation of new social space. Sarah Scott's research (1993a,b), concludes that the traditional elites whose lifestyle included both town and rural estate in the early Empire, withdrew increasingly from town life in the late Empire. Their previous investment in urban monuments and use of public spaces for the exercise of their power and patronage was displaced to their villas, where we see a compensatory investment in prestigious building and the erection of new spaces for the display of wealth and the exercise of power over clients. In other words this is not innovation but merely displacement of elite activity.

If this long era or conjuncture of some 800 to 900 years represents surface variety over underlying all-but-timeless structure, our attention is redirected to those special circumstances in the mature Iron Age when the structure crystallized, and here we might postulate a central role for historically contingent factors.

The English parish church

My final example brings together various strands trailing through this paper: the English parish church. The ninth to thirteenth centuries AD in Western Europe represent one of the most dynamic eras of growth in this region. As we have already seen, the countryside becomes packed with village communities, which although subordinate to minor and major lords, secular and clerical, develop a strong individual sense of semi-autonomy and local management of territory through the corporate community. These crystallizing networks of rural communities are provided with a religious focus through the erection of a parish church, often at the lord's expense.

The evolutionary morphology of parish churches provides another development series through which we can interrogate the directionality or otherwise of history (Figure 7.3). In Richard Morris's outstanding survey of the phenomenon (1989), the acceleration of church construction during the tenth and especially the eleventh century might well deserve Bouwisma's term the 'cataclysmic' transformation of history; Morris himself describes the erection of some 7000 English churches as 'mushrooms in the night', From simple cells appropriate to the 150 or less souls of the eleventh-century village, the typical parish church, as shown in Figure 7.4 in idealized form, expands capacity progressively through the addition of a chancel, nave lengthening, then the construction of one and often two side aisles. The underlying motor

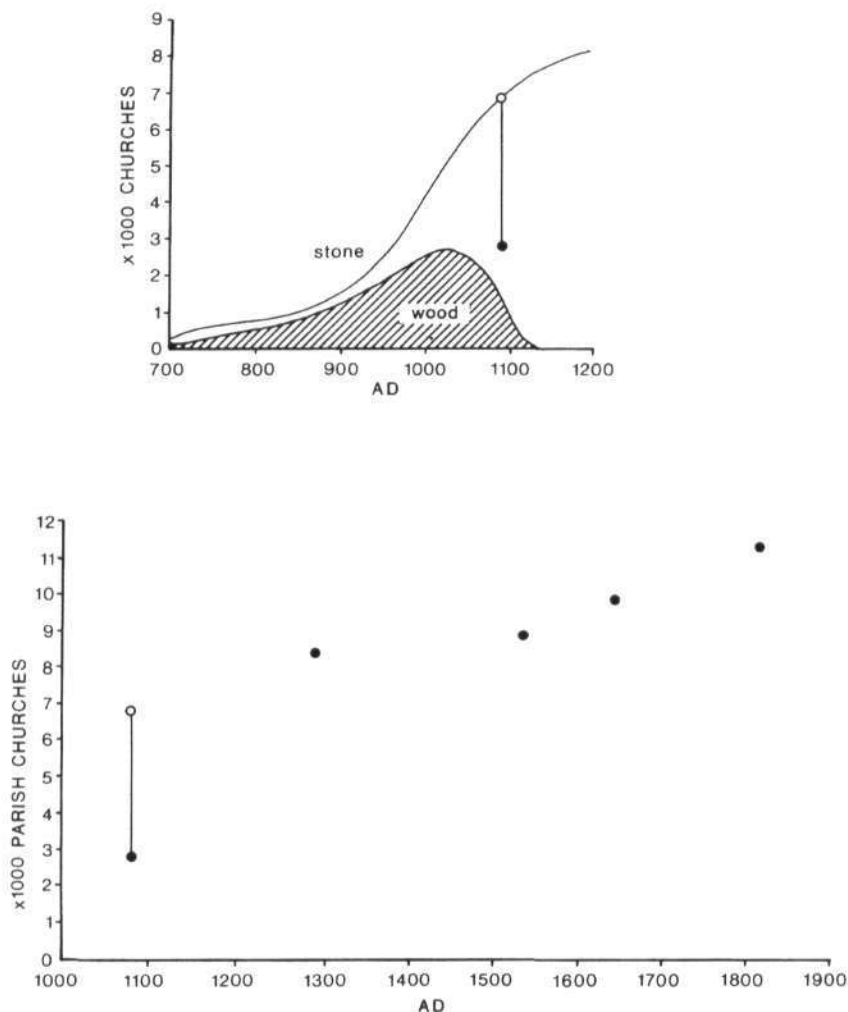
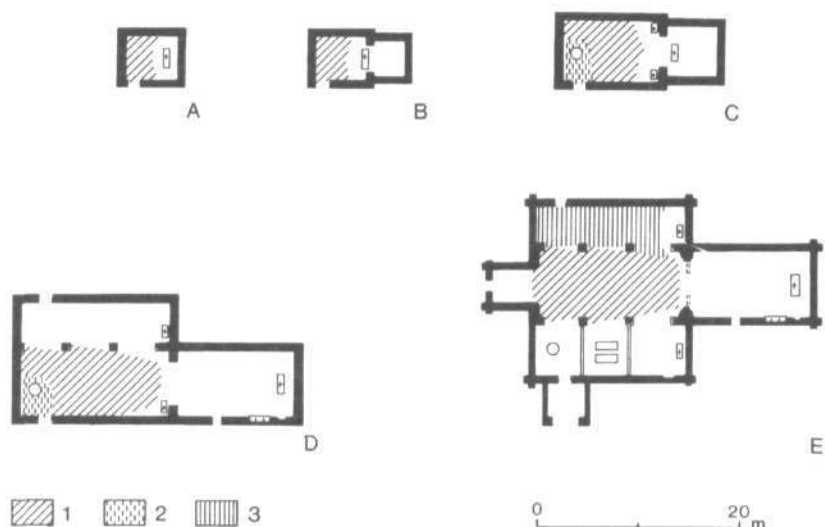


Figure 7.3 English parish church construction (from Morris, 1989, fig. 37)

for enlargement was primarily demographic, as by the early fourteenth century a typical ninth to eleventh-century church would be servicing a parish population two or even three times as large as at its foundation. But the addition of a second aisle was probably historically contingent on the relaxation of dogma which permitted local gentry to create prestigious burial monuments and chantries *within* the body of the church.

From the later fourteenth to the early nineteenth century there appear some of the most characteristic and striking features of the



1. original structure
2. chancel addition
3. side aisle addition

Figure 7.4 Expansion of the typical parish church between *c.* 1000–1400 AD (after Morris, 1989, fig. 90)

parish church: the glorious windows, tracery, towers and other architectural ornaments of the perpendicular style; the lavish investment within the church by generation after generation of local wealthy families in funerary monuments and inscriptions.

But we have passed across the cataclysm of the late fourteenth-century crisis with its plagues, environmental changes, agricultural abandonments, and consequent rural depopulation. We have entered Ladurie's time of timelessness. The underlying historical framework shows a correspondingly different picture to the attractive bustle of activity outside and inside the church. Demographically speaking, from a high mediaeval peak of 4 to 5 million or over 6 million people,⁴ the following 400 years achieve nothing beyond the collapse of population and its reconstitution to a similar level by the eighteenth century (Figure 7.5). After the explosion of church construction during the preceding era, churchbuilding is virtually at a standstill from the late fourteenth to the seventeenth century, and by 1800 parish churches are still only some 11,000 in number compared to the 9000 or so achieved by the High Middle Ages.

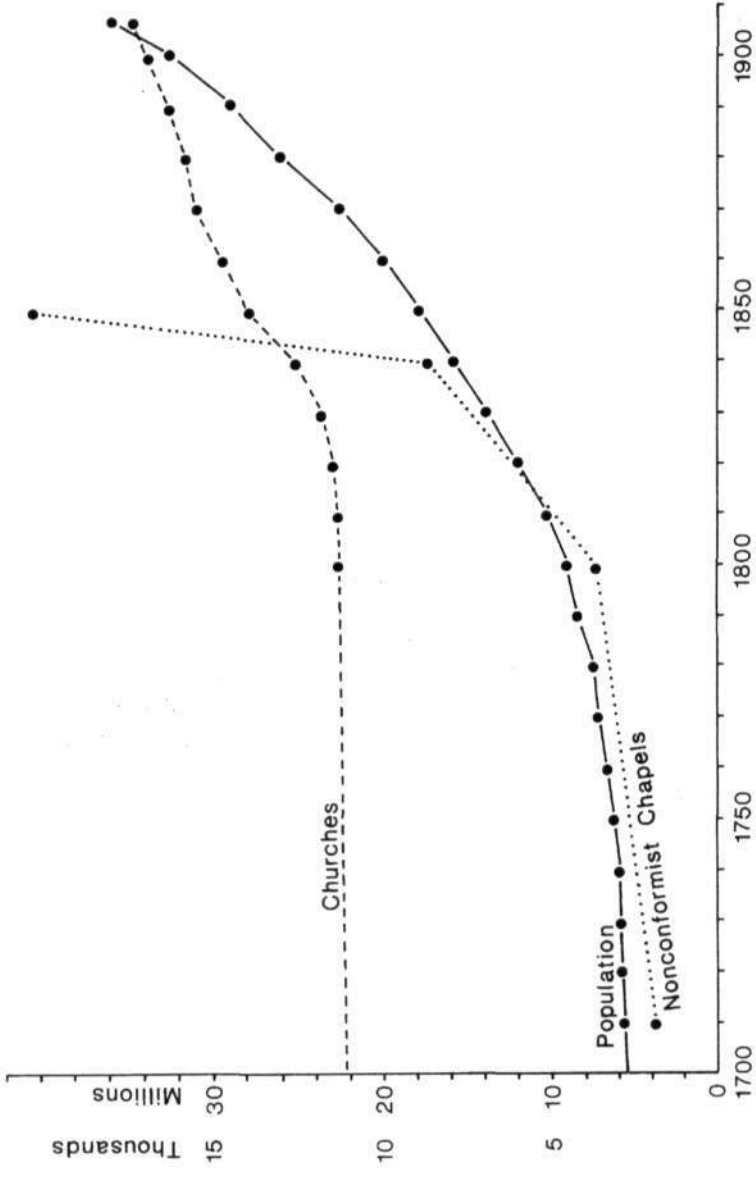


Figure 7.5 Population growth, Anglican (established) church numbers and building of Nonconformist chapels, England and Wales (after Morris, 1989, fig. 110)

Once again the sceptic will object that England's history between the fourteenth century and the early nineteenth century is one of continuous growth and progress, with major advances in agricultural productivity, the steady expansion of urban life, the inexorable expansion since Tudor times of industry and commerce and indeed the rise of market capitalism, the step-by-step advancement of constitutional monarchy and democratic institutions. In this view, which is the long-dominant Whig interpretation of history, the full Victorian flowering of the industrial and commercial might of Britain and the great widening of the franchise achieved by the 1832 Reform Bill follow inevitably from trends visible since the waning of the Middle Ages. Even Ladurie made a possible exception from his blanket timeless structure elsewhere in Western Europe for more dynamic developments in England.

In 1985 this comforting forward-looking vision of English history was shattered in a single tour-de-force volume by the Oxford historian Jonathan Clark: *English Society 1688–1832: Ideology, Social Structure and Political Practice during the Ancien Regime*. This widely accepted piece of revisionism directly challenged the prevalent idea of 'a necessary general direction to the course of social and political change', and by re-analysing the evidence of seventeenth to nineteenth century history provided an interpretation which privileged 'the complexity and flux of human affairs, the subserviency of values to the tactical conjunctures which give them expression, the large role of chance and miscalculation as well as ambition as against purposeful endeavour or anticipations of later alignments' (Clark, *op. cit.*, p. 4).

Far from seeing post-mediaeval English history as unfolding inevitably towards modern democratic liberal capitalism, and much more progressive in this trend than Ladurie's continental oligarchic regimes, Clark emphasizes 'the similarities between England before 1832 and other European social systems of the *ancien regime*' (p. 6). Until 1828–32 England was dominated by a strong and coherent establishment, which was Anglican, aristocratic and monarchical. The *ancien regime* in the eighteenth century, far from weakening, became steadily stronger after the American Revolution, 'and its defeat is no more necessary or inevitable than any other battle' (p. 7). Indeed, enter 'cataclysmic history': 'the events of 1828–32 [the Great Reform Bill and associated bills of toleration and emancipation of Dissenters and Catholics] and their aftermath must strike the eighteenth-century historian as among the most dramatic and profound changes ever effected in English society' (p. 422).

England before the early nineteenth century, from recent research, was nothing like the proto-modern world previously

portrayed: the Industrial Revolution was a major force only from the 1830s and 40s, the giant new cities with their vast anti-establishment populations are a later nineteenth-century phenomenon, political parties were united in support of an elitist establishment, the *nouveaux riches* of commerce and industry were being successfully absorbed into the traditional aristocracy of land, and although average incomes were rising for all, the balance of wealth between the classes in 1800 turns out to have been just the same as in 1688.

From this accumulated evidence Clark rejects the concepts of an inexorable progress of democratic reform and the inevitable transformation of a monolithic establishment oligarchy into a bourgeois-dominated conflict between liberals and conservatives, where liberalism is bound to prevail in the long term. Indeed, by demonstrating that nothing essential had changed by 1800, or even later, Clark is led to seek for unique historical and contingent circumstances to account for the actual course of history in which such a modern society was born: 'There was nothing inevitable about the destruction of the Anglican-aristocratic hegemony in 1828-32, and to explain it we must give priority to political events' (p. 383).

One contingent factor of major importance in toppling the Anglican establishment brings us back to parish churches (Figure 7.5). In retrospect, with dreadful carelessness the Anglican church had ignored the slow build-up of the eighteenth-century population, not just in mediaeval towns but especially in new parts of the countryside through the gradual increase of small-scale industry in villages and new towns; these neglected populations reacted by focusing around the new Dissenting movement, whose chapels, as can be seen, take up most of the population growth till 1850, by which time more than half the church-going population are non-Anglican and therefore non-establishment. Only then, belatedly, does the established and establishment church (wittily satirized as 'the Tory party at prayer') respond with a massive programme of churchbuilding.

Even so, all was not necessarily lost for the establishment in the political battles of 1828-32; rather, Clark argues, a series of chance miscalculations about Catholic and Dissenter emancipation, and the contingent behaviour of key individuals, set up a chain of unpredictable circumstances inaugurating reforms whose implications almost no-one involved could foresee. For Clark, unintentionally a new and modern form of society appeared almost overnight.

Conclusion

Let me conclude with a quote from Stephen Gould:

Our images of evolution are caught in the web of tale telling. They involve progress, pageant; above all, ceaseless motion somewhere. Even revisionist stories that question ideas of gradual progress – the sort that I have been spinning for years – are tales of another kind about good fortune, unpredictability, and contingency. ... But focus on almost any evolutionary moment, and nothing much is happening. Evolution, like ... life itself, is daily repetition almost all the time. ... The fullness of time, of course, does provide a sufficient range for picking out rare moments of activity and linking them together into a story. But we must understand that nothing happens most of the time ... if we hope to grasp the dynamics of evolutionary change. (*Bully for Brontosaurus*, pp. 251–2)

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Notes

1. In general the European countries show only slight overall rises in population between the climax high mediaeval estimates for the early fourteenth century and the figures suggested for the eighteenth century. France in Ladorie's calculations moves from some 17 million to 19–20 million by 1700 over this time period, with – as elsewhere in Europe – an intervening major depression.
2. For discussion of the phenomenon of the rise of the 'corporate village community' in mediaeval Europe see Davies 1988, Fox 1992, Harvey 1989, Rösener 1992, Wickham 1988. Such communities remained central to rural life in many parts of Europe till the early modern era (cf. Freeman 1968 for traditional villages in Iberia).
3. If Fox is correct (1992; cf. also 1981), then the English reorganization of field systems by the village community was time-transgressive, beginning around the tenth century in later Saxon times but still occurring in the high mediaeval era. In northern France and in Germany, however, it appears that similar changes are typically taking place in the twelfth and thirteenth centuries. If this is the case, then major communal decisions were made in England at a stage when the 'Dunbar' face-to-face community was still dominant, as well as later, when population rise in a crowded landscape was accommodated through the rise of the corporate community and its minority superstructure. In other words,

communal reorganization may have occurred both as a mechanism to remove constraints on local growth, and as a forced response to the problems arising from uncoordinated local growth.

4. Intriguingly, Millett (1990) hypothesizes that the population of Roman Britain was greater than that of Domesday times (traditionally 1–2 million) and less than the upper estimates of the high mediaeval era (5–6 million), thus opening up another potential structural recurrence through the similarities between later Iron Age/Roman population density, mature mediaeval density and the population levels prevailing in post-mediaeval times up to the eighteenth century.

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Index

Topics

- adaptive radiation 33-5, 37
Allen's Rule 60
allopatric model, of speciation 37
Alu-chromosome 73
ammonites 14, 18, 21-2, 28
anagenesis xviii, xx-xxi, 2, 9-10,
32-3, 64-5, 77, 79-2, 84-5, 87, 90,
93-4
ancien regime, European 144
Anglo-Saxon Chronicle 15
anoxic events 22, 24
archetypes 32
Aurignacian, industry 69
autosomal nuclear DNA 73
- bacteria xiv
Bayeux tapestry 15
bedding-planes, in strata xvii-xviii, 6,
25
bilateral symmetry xiv
black shales *see* hypoxic
bolide *see* meteor
bovids, African 39
- carnivores 38-9
catarrhines 37-8
Cenomanian chalks 6
chaos, theory 121-2, 128, *see also*
self-organizing
Chatelperronian, industry 69
chimpanzees 104, 108-9, 111-13
church, medieval parish 132, 140-3,
145
cladogenesis, cladistic analysis xviii,
9-10, 33, 37, 44-5, 59, 82,
90
- climatic change 39, 65, 67, 75, 83, 103,
108-9, 118, 120
comets *see* meteor
Companion star, theory of 18
corporate community 136-7, 140,
146
critical realism 119
cyclicality x
- Deccan Trap, volcanism 28
dinosaurs, extinction of x, xix, xxii, 17,
22
Dissenting movement 145
dissipative structures *see* self-organizing
domestication, of plants and animals,
origins of agriculture xvii, 103,
110, 114, 118, 123, 126, 128
Dorfstaat, model 135-6
drift, genetic xix, 10, 63, 67, 77, 79,
86-7, 92, 94
- equilibrium models 120-1, 128
- founder effect *see* drift, genetic
Fourier analysis 20
fractals xiv
- Garden of Eden models 74
geographical barriers, and
speciation 38
gradualism, principle of xix, 43, 45, 85,
90, 146
Green Debate 118-19
greenhouse effect 25
- Halley's Comet 15, 17
Hangenberg Events 24, 28
hunter-gatherers 102-14, 123

- hypoxic, black-shale events 14, 21-2, 24, 28
- ice-ages 27-8
- Industrial Revolution 118, 123, 126-8, 144-5
- iridium anomaly 17
- Kellwasser Event 22, 28
- landnam, colonization model 121
- Malthusian demographic model 133-4
- mass extinctions xix, 10-11, 14-15, 17-18, 20, 24, *see also* dinosaurs
- megadonty 40
- meteor, impact on Earth x, xix, xxii, 17-18, 22, 24, 28
- mitochondrial DNA 72-4
- moral economy, peasant 111
- motionless history *see* timeless history
- narrative, mode of explanation xi-xiii, xviii, 132, 134, 146
- nemesis star, theory of 18
- neocortex, of brain 111
- Ohm's Law 122
- orbital forcing, on Earth's climate 6, 15, 17-18, 25-9
- optimal foraging theory 104
- origins of agriculture *see* domestication, of plants and animals
- ovulation rates 106-7, 114
- parish church *see* church, medieval parish
- periodicity 14-15, 17-18, 20
- plate-tectonics 24
- pleiotropic, gene effects 70
- polis*, ancient Greek city-state 132, 135-7
- positivism x, 119
- progress, principle of xii, xx, 37, 102-3, 111, 120, 132-5, 139, 144-5
- Protestantism 127
- punctuated equilibrium, principle of xvii-xxi, 2, 9-10, 25, 29, 43, 64, 71, 79-80, 83, 85, 90, 134
- random walk xvii, 1, 3, 6-7, 10
- Reform Bill of 1832 144
- Renaissance, the 132-4
- rifting, geological 35
- Roman villa xxi, 132, 137-40
- scientific method x
- sea-level, changes in 15, 17, 20, 22, 24, 35, 62, 105
- sea-urchins 10
- sedimentary cyclicality 15, 25
- selection, directed 7-8, 11, 80, 82
- selection, natural, principle of 3, 36, 39-40, 43, *see also* selection, directed
- self-organizing, dissipative structures 118, 121, 127-8
- speciation xviii-xxi, 33, 37-40, 43-4, 65, 71, 73, 77, 79-82, 84-7, 90, 93-4
- species longevity 36-7
- stasis xvii-xviii, xx-xxi, 1, 3, 7-8, 10-11, 28-9, 79-80, 82, 121, 128
- succession, ecological 121
- sustainability, model 107, 118, 123, 126, 128
- Taghanic Event 28
- timeless history 132-4, 139-40, 142, 144
- transilience, genetic xxi, 78, 86-9, 93-4
- trends, evolutionary 3, 6-7
- varves 6, 29
- villa *see* Roman villa
- village community 136-7, 140, 146
- whales, baleen 8
- Whig, interpretation of History 144
- Y-chromosome DNA 72
- Younger Dryas, era 109-11

Persons, Places

- Aché, people 104
- Allia Bay, hominid finds 52
- Alvarez, L.W. and W. 17, 22
- Arago, hominid finds from 76, 87
- Aramis, hominid finds 52, 75
- Archaic *Homo sapiens* 69-71, 73, 76-7, 83-4, 88
- Ardipithecus ramidus* 33-4, 52, 75
- Atapuerca, hominid finds from 76, 85, 87, *see also* Gran Dolina, Sima de los Huesos

- Australopithecus aethiopicus* 34, 53-4, 57
Australopithecus afarensis 34, 36, 52-3, 81
Australopithecus africanus 32, 34, 36, 53, 57
Australopithecus anamensis 34, 52-3
Australopithecus bahrelgazali 34, 81
Australopithecus boisei 34, 54, 57-8, 109
Australopithecus crassidens 34, 54, 109
Australopithecus robustus 32, 34, 54, 57, 109, *see also* robust australopithecines
- Bach, J.S. xv
 Baringo Kaphthurin, hominid finds from 83
 Barranca Leon, hominid finds from 66
 Batek De', people 113
 Beethoven, L. v. xiv
 Belohdelie, hominid finds 52
 Biache, hominid finds from 87
 Binford, L.R. 105
 Bodo, hominid finds from 67, 83-4
 Border Cave, hominid finds from 71
 Bouwsma, W. 132, 134, 140
 Boxgrove, hominid finds from 66
 Bradley, R. 134
 Braidwood, R. 103
 Broom, R. 54
- Carson, H.L. 85, 87
 Changyang, hominid finds from 83
 Chaoxian, hominid finds from 76, 83
 Childe, G. 103
 Clark, J. 144-5
 Clarke, R.J. 53
 Coalbrookdale, industrial site 127
 Collingwood, R.G. 137
 Cueva Victoria, hominid finds from 66
 Cunliffe, B. 139
- Dali, hominid finds from 65, 71, 76, 83
 Darby, A. 127
 Darwin, C. xiv, xxi, 1-2, 11, 14, 17, 31-2, 43
 Dingcun, hominid finds from 65
 Dmanisi, hominid finds from 60, 62
 Dorobo, people 106
 Drury, W.H. 121
 Dunbar, R. 111-13, 135, 146
- Efe, people 107
 Ehrenberg, M. 111
 Eldredge, N. xviii, 2, 29, 43, 79, 82, 92, 94-5
 Eliye Springs, hominid finds from 71
- Fisher, R.A. 8
 Foley, R. 103, 110
 Fox, H. 146
 Futuyama, D.L. 80, 86
- Gellner, E. 127
 Gidjingali, people 104, 106, 113
 Gingerich, P.D. 5
 Gladysvale, hominid finds from 53
 Goland, C. 102-3, 107-8
 Gould, S.J. 1, 25, 28-9, 36, 43-4, 82, 94-5, 132, 134, 146
 Gran Dolina (Atapuerca), hominid finds from 66-7
 Groves, C.P. 33
 Gussage All Saints, Iron Age site 139
 G/wi, people 113
- Hadar, hominid finds 52
 Hadza, people 113
 Hall, C.A.S. 122
 Harpending, H.C. 74
 Harrison, T. 82
 Hawkes, K. 103-5, 107
 Heidelberg, hominid finds from 66, 76
 Hexian, hominid finds from 65, 76, 83
 Hill, K. 104
 Hole, F. 103, 111
Homo erectus xx, 32, 34, 55-6, 58-67, 75-6, 81-5, 90, 93, 95, 110
Homo erectus soloensis 64
Homo ergaster 34, 55, 59, 62, 75, 82-3, 93
Homo habilis 32, 34, 53-6, 58-9, 62-4, 81, 90, 109-11
Homo heidelbergensis 34, 67, 76, 84-5
Homo neanderthalensis 34, 85, 88, *see also* Neanderthals
Homo rhodesiensis 34, 67, 84
Homo rudolfensis 34, 55, 58-9, 64
Homo sapiens xi, xx, 32-4, 36, 39, 43, 65, 67-70, 73, 76, 88, 90, 92-3, 110
Homo sapiens heidelbergensis *see* *Homo heidelbergensis*
Homo sapiens steinheimensis 67, 76, 84

- Howell, F.C. 33, 63-5
Huang, W. 61
- Isernia, hominid finds from 66
- Jinniu Shan, hominid finds from 71, 76, 83
- Jones, E.L. 127
- Kabuh-Notopuro, hominid finds from 82
- Kabwe (Broken Hill), hominid finds from 67, 71, 83-4
- Kalahari Desert 110
- Kanapoi, hominid finds 52
- Kebara, hominid finds from 67
- Kikuyu, people 106
- Kirsten, E. 135
- Klasie's River Mouth, hominid finds from 71
- Klein, R. 57
- Koobi Fora, hominid finds from 55
- Kromdraai, hominid finds from 54
- Kubu, people 105
- Kung, people 104, 106, 112, 113
- Ladurie, E. L. R. 132-4, 136, 139, 142, 144, 146
- Laetoli, hominid finds from 52, 71
- Lande, R. 5, 8
- Lantian, hominid finds from 64
- Lese, people 107
- Levi-Strauss, C. xii, xv
- Longgupo Cave, hominid finds from 61-2, 66
- Lothagam Hill, hominid finds 52, 75
- Maba, hominid finds from 65, 84
- Maka, hominid finds 52
- Makapansgat, hominid finds from 53
- Marx, K. ix
- May, R.M. 122
- Mayr, E. 8, 32, 85-6
- Mbuti 112
- McClaren, D. 22
- McConiston, J. 103, 111
- Meganthropus* 64
- Milankovitch, M. 27-8
- Millett, M. 137, 139, 147
- Modjokerto, hominid finds from 61
- Morris, R. 140
- Mozart, W.A. xiv
- Myers, F. 112
- Nariokotome, hominid finds from 59
- Narmada, hominid finds from 65, 84
- Natufians, cultural group 110, 112
- N'Dele Aka, people 113
- Ndutu, hominid finds from 83-4
- Neanderthals xv, 36, 67-70, 76-7, 84-5, 87-8, 93, 95, *see also Homo neanderthalensis*
- Ngandong (Solo), hominid finds from 64, 76, 83, 85
- Nisbet, I. 121
- North Gill, pollen site 124
- Nuauulu, people 104
- O'Connell, J. 103-5, 107
- Odum, E. 120
- Olduvai, hominid finds from 54, 59-60, 63, 83
- Omo Valley, hominid finds from 53-4, 71, 88
- Paranthropus* 54, 108-9
- Paul, St xv
- Petralona, hominid finds from 76
- Pilbeam, D. 32
- Pimm, S.L. 122
- Pintupi, people 112
- Pope, G.C. 65
- Prigogine, I. 127
- Qafzeh, hominid finds from 67, 71
- Rak, Y. 57
- Raup, D. 17, 20-1
- Richmond, I. 137
- robust australopithecines xx, 33-4, 36, 40, 55-6, 58, 63, 75, 108-11, 113-14, *see also Australopithecus robustus, boisei, aethiopicus*
- Rowe, A.W. 6
- Saldana, hominid finds from 71
- Sambungmachen, hominid finds from 64
- Samburu, people 106
- Sangiran, hominid finds from 61, 64, 66
- Scott, J. 111
- Scott, S. 140
- Sepkoski, J.J. 17, 20-1
- Shanidar, hominid finds from 67

- Sheldon, P.R. 2, 8, 10
 Sima de los Huesos (Atapuerca) 66, 68, 76
 Simpson, G.G. xix
 Skhul, hominid finds from 67, 71
 Smith, E.A. 106
 Smith, F.H. 70
 Soleilhac, artefact site 66
 Spengler, O. x
 Stanley, S.M. 85
 St Cesaire, hominid finds from 69
 Steinheim, *see Homo sapiens steinheimensis*
 Stengers, I. 127
 Sterkfontein, hominid finds from 53-4
 Swartkrans, hominid finds from 54-5, 57
 Swisher, C.C. 61
- Tabarin, hominid finds 52, 75
 Tabun, hominid finds from 67
 Tainter, J. 128
 Tattersall, I. 67, 84, 95
 Taung, hominid finds from 53
 Templeton, A.R. 86-7, 95
 Thetford, Iron Age site 139
 Tishkoff, S.A. 73-4
 Tollard Royal, Iron Age site 139
 Toynbee, A. x
 Trivers, R. 105
 Turkana, Lake, hominid finds from 54-6, 58, 76
 Turnbull, C. 112
- Turner, A. 66-7
 'Ubeidiya, hominid finds from 60
- Vallonet, Le, artefact site 66
 Venta Micena, hominid finds from 66
 Vrba, E. 39, 108
- Wallace, A.R. 31
 Weldon, W.F.R. 3
 West Turkana, hominid finds from 53
 Wiessner, P. 112
 Willey, G. 103
 Williams, E. 103
 Winterhalder, B. 102-3, 107-8
 Wolfendale, A. 18
 Wolpoff, M.H. xx, 90, 93
 Wood, B.A. 33, 40, 59, 109
 Wright, population model 79, 87
 Wynne-Edwards, V.C. 104-6
- Xujiayao, hominid finds from 65, 71, 76, 83
- Yankunyjatjajara, people 113
 Yanomama, population model 87
 Yunxian, hominid finds from 65
- Zhang, Y. 82
 Zhoukoudian, hominid finds from 60, 64-5, 76, 82-3
 Zubrow, E. 69