

Species diversity in human evolution: challenges and opportunities

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Over the last 150 years the number of hominin fossils discovered has increased, and with it the taxonomic diversity recognised. There are currently claims for at least 26 hominin species. I consider here the challenge posed by this diversity, and how we can determine, through comparative modelling, whether it is a real evolutionary signal or an artefact of our procedures, and also the opportunities provided to make the science of human evolution a more comparative one.

INTRODUCTION

When Phillip Tobias was born in 1925, the only known extinct hominin species, leaving aside *Eoanthropus dawsoni*, were the Neanderthals, *Pithecanthropus erectus*, now *Homo erectus*, and *Homo heidelbergensis*. By either coincidence or destiny, his birth also coincided with the beginnings of the great adventure of African fossil hominin discoveries, for 1925 saw the announcement of the *Australopithecus africanus*. Eighty years later there are now some 26 recognised species, placed into six or seven genera. While many, including Tobias, might dispute this exact number and wish to revise it downwards, there is no doubt that the evolutionary history of our lineage is far more speciose than previously thought (Brace, 1967; Wolpoff, 1971).

Much of the discussion in palaeoanthropology in recent years has focused on whether these taxa, often represented by a few fragmentary specimens, are genuine biological species, and what their relationships to each other might be (Tattersall, 1986; Foley, 1991; Fleagle 1995; Conroy, 2002; Hunt, 2003). According to definition, trait selection and method of analysis, the exact number can be pushed up or down. However, even the most severe of tests will only reduce the number to around 15. This is a far cry from the three or four species seen in the classic phylogenies that were based on Mayr's (1950) seminal classification, that shaped so much of later twentieth century palaeoanthropology. It also contrasts with the three or four known African ape species today.

It can be argued that the growth of hominin diversity, discovered through the fossil record, represents the greatest challenge to the study of human evolution, requiring us to look at the problem in new ways. I would also suggest that this higher diversity also offers the discipline the opportunity of being far more comparative, and to be more closely aligned to the rest of evolutionary biology, than the essentially anagenetic approach that has characterised so much of human evolutionary studies. It is this diversity, which over the course of a long and distinguished career, Phillip Tobias has done so much to establish, which will be the focus of the next decade's research, and furthermore, which is likely to maintain the value of a fossil-based approach to human evolution in the context of the growth of molecular genetics.

HOMINIM DIVERSITY: THE EVIDENCE

Table 1 shows the range of hominin taxa that have been described (Foley, 1998; Foley, 1999a,b; 2001; Tattersall, 2000; Wood & Richmond, 2000). A number of points can be made about this. First, that the increase in hominin diversity has been

associated with an extension of time range of the lineage. In terms of current chronology, hominin origins at the beginning of the twentieth century would have been placed at between one and two million years. Assuming *Sahelanthropus* is indeed a hominin (Brunet *et al.*, 2002), then this would be very close to the last common ancestor with *Pan*, estimated on molecular grounds to lie between 5 and 8 million years ago (Ruvolo *et al.*, 1991). Thus the hominin fossil record has quadrupled in age since the last 100 years, and the increase in hominin diversity is thus to be broadly expected. Second, the observed diversity is not just occurring among the earlier forms – the australopithecines and allies – which are generally considered to be rather ape-like, and so might be expected to be more speciose than humans, but is also found in the genus *Homo*.

THE CHALLENGE OF HOMINIM DIVERSITY: ARTEFACT OR USEFUL EVOLUTIONARY INFORMATION?

Perhaps the greatest challenge posed by the rise in hominin diversity is determining whether it is 'real', and can thus be used for evolutionary inference, or whether it is an artefact of either preservation or the approaches to classification. We can tackle this question, at least partially, by considering whether the nature of the signal is consistent with what we expect on the basis of comparison with other lineages, or the expectations of evolutionary principles. Four such signals can be examined briefly here – numbers of species per genus; species longevity, geographical distribution, and the pattern of discovery.

Turning first to the relative diversity of genera, from Table 2 it can be seen that *Homo* has the most recognised species (12), followed by *Australopithecus* (5) and *Paranthropus* (4) (nine together if these genera are lumped). All of the early genera are characterised by one or at most two species, despite the fact that they probably were in existence for at least similar lengths of time as the better known and later genera. This observation would suggest that there is an underestimate of earlier diversity, and that we should probably expect the discovery, across the terminal Miocene and earlier Pliocene, of more species, and in particular ones that exhibit a high degree of variation relative to later hominins. Indeed, as we are already discovering, these new genera are leading to a reconsideration of the classic division between chimpanzee-like and human-like lineages. The most probable conclusion is therefore that there is an underestimate of diversity in the earlier periods, although it should not be ruled out – indeed would be an important area for future research – that in the early divergence of the African ape/human clade there was very rapid adaptive and

Table 1. Hominin diversity observed in the fossil record. This lists all the taxa which are currently recognised by some authors, showing their approximate date of first appearance and geographical distribution. The status of many of these is often controversial, with some arguing for a reduced number and suppression of various taxa.

Genus	Species	Abbreviation. (Figure 1)	First appearance	Distribution	Notes
<i>Sahelanthropus</i>	<i>S. tchadensis</i>	tch	~7.2	Found in Chad	Possibly the first hominin, but affinities have been widely debated. If it is a hominin then it must lie very close to the origins of the separation from <i>Pan</i> .
<i>Orrorin</i>	<i>O. tugenensis</i>	tug	~6.0	Found in the Tugen Hills, central Kenya.	Fragmentary specimens only, but with possible hominin traits, including bipedalism.
<i>Ardipithecus</i>	<i>A. kababba</i>	kab	~4.9	Found in the Middle Awash Valley, Ethiopia.	Some regard this as an early form of <i>A. ramidus</i> .
	<i>A. ramidus</i>	ram	~4.4	Found in the Middle Awash Valley, Ethiopia.	Fragmentary specimens only published so far, and with some hominin and some more primitive traits.
<i>Kenyanthropus</i>	<i>K. platyops</i>	plat	~3.5	Known from Northern Kenya	Single fragmentary specimen published, and status uncertain, possibly with affinities to <i>H. rudolfensis</i> .
<i>Australopithecus</i>	<i>A. anamensis</i>	ana	~4.2	Found at Alia Bay and Kanapoi in Northern Kenya	Well-documented as clear homin, with substantial evidence for bipedalism.
	<i>A. afarensis</i>	afa	~3.9	Distributed across eastern Africa, and known especially from Hadar, Ethiopia, and Laetoli, Tanzania	Well-known and described species, exhibiting considerable variation that some ascribe to sexual dimorphism, others to taxonomic diversity.
	<i>A. africanus</i>	afr	?3.3	Gauteng, Limpopo and North West Provinces of South Africa (Sterkfontein, Makapansgat, Taung)	Well documented species, although some argue that the total material may represent more than one species.
	<i>A. gahri</i>	gah	~2.5	Found in Bouri, Middle Awash, Ethiopia only.	Associated with bones containing cutmarks, and therefore may be one of the earliest toolmakers.
	<i>A. bahrelghazali</i>	bah	~3.5–3.0	Known from Chad.	Known from one site only, and important for extending the geographical range of the australopithecines towards central and western Africa.
<i>Australopithecus</i> (<i>Paranthropus</i>)	<i>A. (P.) aethiopicus</i>	aet	~2.5	Known from northern Kenya (Lomekwi) and Ethiopia (Omo Valley)	Many authorities prefer to raise this group to generic level (<i>Paranthropus</i>), but there have been questions raised about its monophyletic status.
	<i>A. (P.) boisei</i>	boi	2.45	Widespread over much of eastern Africa, from Ethiopia (Middle Awash) to northern Tanzania (Olduvai)	The earliest recorded 'robust' australopithecine.
	<i>A. (P.) robustus</i>	rob	~2.0	Known from Gauteng Province, South Africa (Kromdraai, Drimolen)	Generally viewed as the most derived and specialised of the robust australopithecines.
<i>Homo</i>	<i>A. (P.) crassidens</i>	cra	~2.0	Found at Swartkrans in Gauteng Province, South Africa.	Most authorities would place all the material from South Africa that is 'robust' into a single species (<i>A. robustus</i>), but some have made a case for separating <i>A. crassidens</i> .
	<i>H. habilis</i>	hab	~2.0	East African distribution, especially Kenya and Tanzania	There has been debate as to whether this taxon should be defined narrowly, or more widely to include <i>H. rudolfensis</i> .
	<i>H. rudolfensis</i>	rud	~2.4	East African distribution, possibly extending to Malawi	There has been considerable controversy concerning these taxa, with some questioning whether they belong in <i>Homo</i> or <i>Australopithecus</i> .
	<i>H. ergaster</i>	erg	~1.7	Known from East Africa, and most probably extending to South Africa.	This taxon has been viewed by some as a part of a broader <i>H. erectus</i> clade.

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Table 1 (continued)

Genus	Species	Abbreviation (Fig. 1)	First appearance	Distribution	Notes
<i>Homo</i>	<i>H. erectus</i>	ere	1.9 or 1.0	Distributed across eastern and southeastern Asia, and depending upon definition, may also have existed in Europe and Africa	One view is that this is a very wide ranging taxon of the Lower and Middle Pleistocene, while to others it is a specifically Eastern Asian clade.
	<i>H. georgicus</i>	geo	1.6	Known from the site of Dmanisi in Georgia	Conventionally seen as having affinities with <i>H. ergaster</i> , but more recent finds have shown more variability.
	<i>H. antecessor</i>	ant	0.8	Found at Atapuerca in Spain	A controversial taxon which is based on a single immature specimen, but which may indicate a unique European taxon.
	<i>H. cepranensis</i>	cep	0.9–0.74	Found at Ceprano in Italy.	Based on one specimen, this has been seen as having affinities to both Asian <i>H. erectus</i> and <i>H. ergaster</i> .
	<i>H. heidelbergensis</i>	hei	0.7	Distributed across Africa and Europe, and possibly extended to Eastern Asia	Formerly referred to as 'archaic <i>H. sapiens</i> '; this taxon has also been divided into European (<i>heidelbergensis</i>) and African (<i>rhodesiensis</i>) lineages.
	<i>H. helmei</i>	hel	0.3	Distributed across Africa, and putatively in Europe	Proposed by some as a larger brained hominin that is ancestral to both <i>H. neanderthalensis</i> and <i>H. sapiens</i> .
	<i>H. neanderthalensis</i>	nea	0.2	Widespread Eurasian distribution.	This taxon has been subject to many different interpretations, but is now used to describe a specific Eurasian later Pleistocene lineage
	<i>H. floresiensis</i>	flo	?0.09	Known from the island of Flores in Indonesia	Recent discovery of an insular pygmy hominin, most probably with affinities to <i>H. erectus</i> .
	<i>H. sapiens</i>	sap	0.16	Earliest forms in Eastern Africa (Idaltu and Omo Kibish in Ethiopia), then has increasingly widespread and ultimately global distribution	Generally now taken to mean anatomically modern humans, but has historically been defined more broadly.

morphological divergence with relatively little speciation – in contrast to later human evolution, when there was considerable speciation, but relatively little morphological change and adaptive change. It could perhaps also be argued that, on the basis of an average of 3.6 species per million years for all hominins, the genus *Homo* has rather more species than would be expected (5.2 per million years).

The second way of looking at whether the signal of evolutionary diversity is real is by considering geographical distribution; all the genera have their origins in Africa, and all except for *Homo* are entirely confined to Africa on the basis of current evidence. It could be argued that this is a reflection of the scale of work carried out in recent years in Africa, or the nature of the geological record. This is a perennial problem, but given the increasing evidence for the African origin of hominins on both fossil and genetic grounds, and the fact that most primate genera are in fact confined to only one continent (Wolfheim, 1983) (the only extant exceptions being *Papio* and *Macaca*, and the only known extinct example being *Theropithecus* (Pickford, 1993), then the geographical consistency of the hominin fossil record may well be of significance.

A third approach is to assess the pattern of diversity against the expected longevity of the species. Figure 1 shows the known chronological range of the species. Those species for which there is only one known specimen have been given an arbitrary range which broadly speaking reflects the chronological resolution of the dating. *H. sapiens* is artificially truncated at approximately 0.2 Myr as it is not yet extinct. As can be seen, the longest surviving taxon is *Australopithecus africanus* (1.3 Myr) and six of them have durations of one million years or more. The average longevity of the species for which there is a genuine range is 0.9 ± 0.41 Myr (range = 0.4–1.7 Myr), which compares well with mammalian averages that fluctuate around one million years (Stanley, 1979).

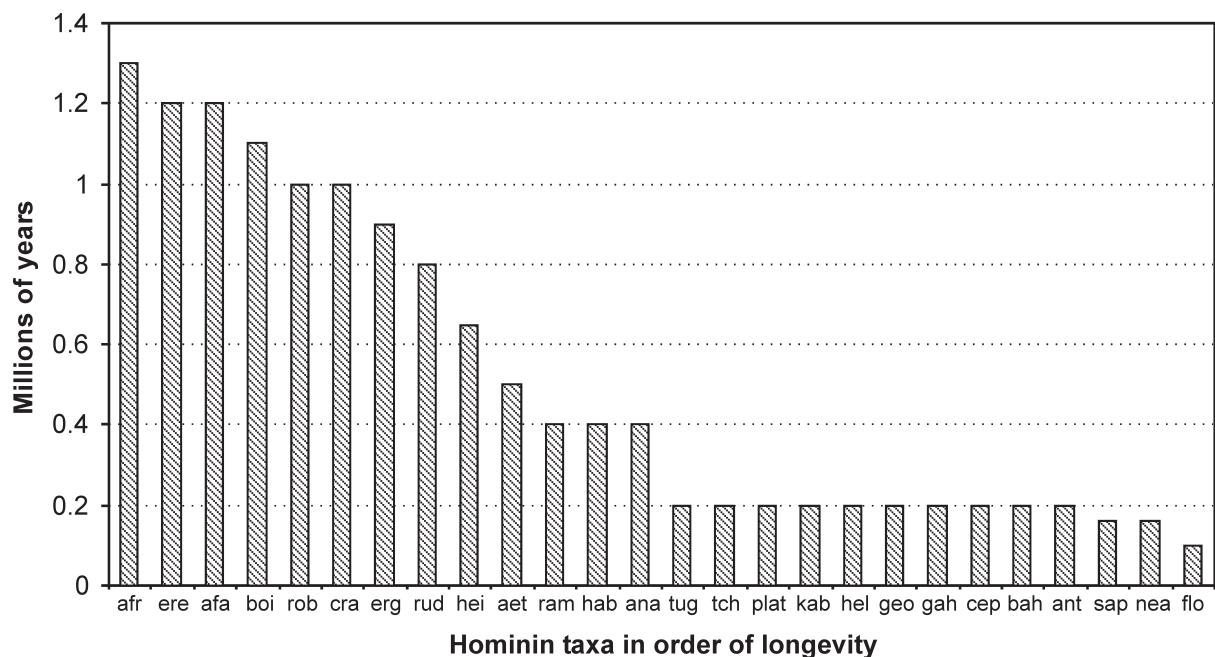
Clearly, the fact that so many hominin taxa – around 10 – are based on only one locality and sometimes one specimen is a matter of considerable concern, and must undermine our confidence in levels of hominin diversity, although it is unlikely that further specimens will reduce the number.

Finally, we can consider hominin diversity in the context of the pattern of discovery. Figure 2 plots the number of fossil species 'recognised' against the history of discovery over the last 150 years. In terms of whether the current estimate of around 25 is correct, it can be seen that the rate of discovery has rapidly increased in the last half-century, and there is no sign of an asymptote. To this extent, it may be proposed that we are still underestimating the number of hominin species.

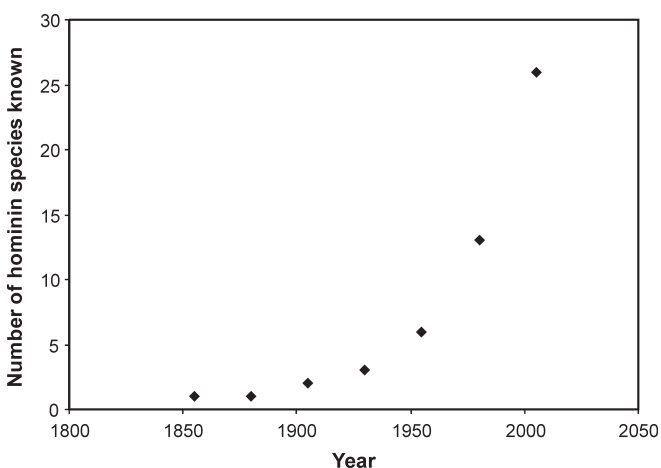
In considering the extent to which our knowledge of hominin evolutionary diversity is a challenge to how confident we are that the pattern is 'real', we come away with a conclusion of moderate confidence. That we are underestimating the earlier periods is suggested by the way in which the Pliocene genera are species poor compared to the later

Table 2. Comparative and relative diversity of the fossil hominin taxa by genus and larger groupings.

Group	Genus or subgenus	Number of species	% Hominin species	Species per million years
Ape-like hominins		4	15.4	1.4
	<i>Sahelanthropus</i>	1	3.8	–
	<i>Orrorin</i>	1	3.8	–
	<i>Ardipithecus</i>	2	7.6	1.33
Australopithecines and allies		10	38.5	3.1
	<i>Kenyanthropus</i>	1	3.8	–
	<i>Australopithecus</i>	5	19.2	2.3
	<i>Paranthropus</i>	4	15.4	2.7
<i>Homo</i>	<i>Homo</i>	12	46.2	5.2
All hominins		26	100	3.6

**Figure 1.** Longevity (first appearance datum – last appearance datum) of hominin species, organised in order of longevity. See Table 1 for abbreviations.

Pliocene and Pleistocene ones, and that we are still on a sharply increasing curve of discovery might also indicate that the full diversity is not yet known even for later periods. What is almost certainly not the case is that we are overestimating diversity.

**Figure 2.** Number of hominin species discovered and recognised over the last 150 years.

Various attempts have been made to predict the number of species of hominin likely to have occurred. On the basis of body size, Conroy has claimed that hominin evolution should be relatively species poor (Conroy, 2002); Hunt (2003), using comparisons across a broad spectrum of adaptive traits among primates and their relationship with speciosity also argued for few species (no more than two at any one time). However, Foley (1991), using models based on primate diversity in relation to geographical range size and evolutionary rates, proposed levels of speciosity that match the fossil record well, and are also related to adaptive patterns. Fleagle (1995) has also argued that the higher number of fossil hominins is in line with expectations of primate diversity.

OPPORTUNITIES

If comparatively high levels of hominin diversity – comparative, that is, to the expectations of the anthropologists working in the middle part of the twentieth century – are empirically robust and theoretically consistent, then we can ask the question – what opportunities does this now provide for palaeo-anthropology and the understanding of human evolution? More broadly, how can it provide insights into the evolutionary process as a whole.

Perhaps the best way to consider what the opportunities offered by higher levels of hominin diversity is to ask the simple question, what is happening, evolutionarily and ecologically, when the number of species in a lineage increases?

It is tempting to give the equally simple answer to this question, namely that speciation is occurring, but this is largely tautologous, and a better answer is that the conditions necessary for divergence are predominant. Central to these conditions is that of small populations that are isolated one from another. The higher than previously expected levels of hominin diversity implies that most hominin species were prone to isolation of their constituent populations; this in turn suggests that there were limits to their ability to cross barriers (mountains, rivers, oceans), and also that in some cases they were confined to particular habitats. It is only relatively late in human evolution that such barriers were effectively removed. A second possibility is that hominin species were effective competitive barriers to other hominins, and that isolation may have been the product of competitive exclusion. Finally, it is also the case that levels of diversity vary with adaptation – carnivores, for example, are less speciose than herbivores (Foley, 1991) – and so as hominin behaviour changes there may well have been alternations in the conditions liable to lead to speciation.

It follows from this that hominin populations may well have been relatively small (hence promoting isolation), fragile to environmental change, and prone to extinction. This would certainly be consistent both with our observations of the fossil record (Lahr & Foley, 2001), and also with new insights into population bottlenecks arising from evolutionary molecular genetics (Rogers & Harpending, 1992).

Another opportunity provided by higher species diversity is that the overall patterns and trends of hominin evolution can be viewed as a series of adaptive radiations, rather than as a *scala naturae* up which our ancestors climbed. Certainly there is an arrow of time running through these adaptive radiations, which shows that across the longer term such traits as brain size enlarged and geographical distribution was increased, but this occurred in the context of smaller scale expansions and contractions, with the ebb and flow of evolutionary success and failure. Higher species diversity allows us to see this microevolutionary process in more detail, and also to make comparisons across to other contemporary lineages – for example the large cats, which underwent similar radiation, or the terrestrial cercopithecines. As understanding any evolutionary problem must in the end be based on comparisons, the increased number of species found in the hominin record greatly enhances our ability to make such comparisons, and thus draw conclusions about evolutionary pattern and process.

Finally, we can mention one further opportunity that the growing diversity of hominin evolution offers, one that is almost certainly close to Phillip Tobias's heart. The last two decades has seen the expansion and flowering of molecular evolutionary genetics, providing a wealth of information into human evolution that had for long seemed impossible – estimates of population size, differences in evolutionary history between males and females, locating genes that may pinpoint the origins of languages, and much more. To some it may seem that the value of the fossil record diminishes with the discovery of each new single nucleotide polymorphism. However, far from it; to evolutionary genetics this wealth of diversity, of lost species, and ways of life that no longer exist, are invisible. While the processes of human evolution may increasingly be revealed through our genes, the diversity of the hominin fossil record is still the only source of information about the complexity of the pattern of our history.

BUT WHAT IS A SPECIES?

This discussion has been extremely positive about the number of species that are now known in the hominin fossil record, and the opportunities for serious evolutionary science that this can lead to. However, I have been deafeningly silent on one key aspect – namely, what exactly is a species, or more precisely, what sort of species were these multitude of hominin types. The conventional answer would be that they were reproductively isolated one from another, and that they could not interbreed, and thus adhere to the biological species concept (BSC) (Mayr, 1963). This was the model used by Hunt to limit the number of hominin species (Hunt, 2003). However, it is very unlikely that the species described here are genuine BSC species; this is partly an inference drawn from the observation that we know that the levels of potential inter-breeding between perfectly 'good species' are quite high, and that species are not the genetically sealed units that theoretically they should be. Better than asking 'could they have interbred?' it is perhaps more useful to ask – 'did they interbreed?', and the suggestion one would make is that, in terms of the impact of such interbreeding on subsequent generations, almost certainly not. Thus when we talk about high species diversity among hominins, it is not necessarily the case that there are a large number of completely reproductively isolated populations, but that their demographic structure is such that those populations evolved along independent evolutionary trajectories. In practice this is much closer to Simpson's definition of a species (Simpson, 1953) than to that of Ernst Mayr, and to Howell's concept of a palaeodeme (Howell, 1999).

The second reason for not linking this high level of diversity to the Biological Species Concept is that when we are dealing with the flow of populations across time, then clearly there cannot be absolute boundaries that form true species – one must evolve into another at some point, and our fossil sample represents snapshots along this multi-lineage continuum – in some cases the samples may be true terminal points, in others, closer to a shared ancestry. As such, when dealing with the fine-grained, microevolutionary process that we can now observe through the wealth of the hominin fossil record, we should treat species not as absolute biological entities, but as useful analytical units which can help us understand the pattern and process of evolution.

Whatever the level of taxonomic diversity settled upon, and whatever the nature of the species concepts used, however, what we can say is that across the course of Phillip Tobias's career, and to which he has contributed in no small way, the greatest revelation has been the discovery of the diversity of our past, that allows us to explore human evolution in the comparative context of evolutionary biology more fully.

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