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REVIEW

Reticulate evolution and the human past: an anthropological perspective

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Abstract

Context: The evidence is mounting that reticulate (web-like) evolution has shaped the biological histories of many macroscopic plants and animals, including non-human primates closely related to *Homo sapiens*, but the implications of this non-hierarchical evolution for anthropological enquiry are not yet fully understood. When they are understood, the result may be a paradigm shift in evolutionary anthropology.

Objective/methods: This paper reviews the evidence for reticulated evolution in the non-human primates and human lineage. Then it makes the case for extrapolating this sort of patterning to *Homo sapiens* and other hominins and explores the implications this would have for research design, method and understandings of evolution in anthropology.

Results/conclusion: Reticulation was significant in human evolutionary history and continues to influence societies today. Anthropologists and human scientists—whether working on ancient or modern populations—thus need to consider the implications of non-hierarchic evolution, particularly where molecular clocks, mathematical models and simplifying assumptions about evolutionary processes are used. This is not just a problem for palaeoanthropology. The simple fact of different mating systems among modern human groups, for example, may demand that more attention is paid to the potential for complexity in human genetic and cultural histories.

Keywords

Agency, complexity, heterarchy, hybridization, palaeoanthropology

History

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Introduction

Anthropology, the study of humankind, has many sub-fields. Palaeoanthropology studies how hominin anatomies, ecologies and behaviours changed through time and why these changes came about. This locates it at the interface between the human sciences and biology and suggests that a better understanding of evolution—both in general terms and in the specific case of the hominins—would improve our reconstructions of the human biology of the past. Developing this better understanding requires that we periodically revisit our assumptions about the tempo, mode and pattern of evolutionary change in the hominin lineage in light of the ever-improving evidence about our history.

Before the emergence of the modern synthesis, natural history was shaped by Linnaean classification. This structure is characterized by a cascade of one-to-many links between taxa, all pointing in the same direction: each genus can contain many species, and each species many instances or individuals, but every instance belongs to one and only one species and every species to one and only one genus. This hierarchical structure can be extended to families, orders, classes and beyond without loss of generality.

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Hierarchies introduce a measure of logical redundancy into a taxonomic schema. It is enough, for example, to know that the pelvis recovered from an excavation belonged to a human to infer that the organism it came from was also a hominin, a primate, a mammal and a vertebrate, possessing the traits those diagnoses imply. Later 19th century evolutionists linked these hierarchic information-systems to the evolutionary process, treating taxonomic hierarchies as if they were phylogenetic trees and vice versa, but the connection was never clear-cut.

The stick-slip pattern of evolution that Huxley (1864) called ''saltation'' and 20th century biologists called ''punctuated equilibria'' (Gould & Eldredge, 1977) creates a fossil record in which taxa appear suddenly and an explosion of diversity creates a rich mosaic of varieties, species and genera. It is often possible, in these circumstances, to construct a stable taxonomic hierarchy, but harder to justify using it as a proxy for an evolutionary tree.

Among angiosperm plants, for example, the fossil record suggests an explosive radiation of orders, families and genera. Morphologists were obliged to divide attributes into ancestral and derived traits and make evolutionary inferences on theoretical, rather than empirical grounds. More recent work intended to link taxonomy and evolution (see, for example, APG, 2003) has been heavily dependent on genetic analysis. The genetic data can be taken as empirical facts, but the

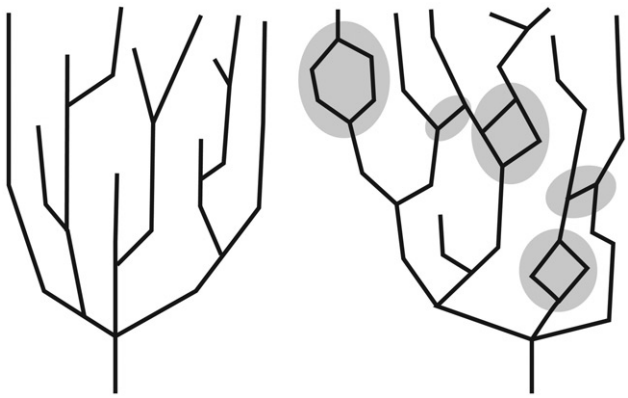

Figure 1. Hierarchic evolution (left) generates a cladogram-like cascade of one-to-many links; heterarchic or reticulated evolution (right) permits lineage re-connections and post-divergence interactions in the network.

analytical methods used to interpret them presume the existence of discrete clades and demes, effectively imposing an assumption of hierarchy on the system.

The hierarchic theory of evolution (Figure 1, left) has assumed a special place in biology and become so deeply embedded that some anthropologists have come to think of it as the norm (see, for example, Gundling, 2010; Tattersall, 2000, and compare with Foley, 2001; Jolly, 2009). In situations where the hierarchic theory holds, the genetic evidence trumps all other sources of evolutionary information and hierarchies constructed from genetic evidence can be used as proxies for phylogenetic trees.

The gene-centred approach looks much weaker if one considers the possibility that taxa may be locally polyphyletic. Different sources of evidence would suggest different evolutionary stories, not because we were using the wrong methods, but because non-hierarchic gene flow has occurred. Concepts like deme or clade would not actually be meaningful at these hot-spots in the evolutionary past. If this hypothesis were correct, then genetic data would be one information source among many in an irreducibly complex signal.

The hypothesis that a taxon is evolutionarily complex can be tested empirically. It implies that hybridization between isolated populations, although rare, is possible and that the morphological data, even if organisms can be arranged hierarchically, cannot be linked to observable trends in the fossil record or to genetic data. It also suggests convergent and divergent evolutionary patterns, punctuated with hybridization events.

The hierarchic model, on the other hand, would be a better fit in situations where the evidence from several sources all suggested the same evolutionary story. Once a well-defined taxon (a family, say, or order) has emerged, it is often possible to interpolate an evolutionary trajectory by treating species as groups of individuals with a shared ancestor, genera as groups of species, ditto and so on, thus reconciling the taxonomic hierarchy to the fossil record and the genetic evidence.

We need a name for complex, non-hierarchic situations. Some social anthropologists (e.g. Crumley, 1995) have used the word *heterarchic*, while geneticists and biologists generally prefer *reticulate* (Arnold, 2009; Sosef, 1997). We treat these as broadly equivalent terms. Reticulate evolution is represented by a network of cross-cutting lineages, characterized by knots of many-to-many links (Figure 1, right). An inter-specific hybrid, for example, would generate a many-to-many knot at the heart of an evolutionary hierarchy and the resulting heterarchy cannot be reconciled to the conventional Linnaean model. Whereas in a hierarchic system each species inherits the unique identity of its genus and family, reticulating lineages have ambiguous inheritance patterns.

An individual cannot be assigned to a unique species if it is the product of a mating across species boundaries, as, for example, in the case of baboon hybrids between *P. hamadryas* and *P. anubis* or *P. anubis* and *P. cynocephalus* (Alberts & Altmann, 2001; Phillips-Conroy & Jolly, 1986). Re-classifying the parents into a single species would simply shift the reticulated pattern down a level in the hierarchy, it wouldn't erase it. Among primates, reticulation seems to be commonest at lower taxonomic grades, i.e. between isolated populations, sub-species, varieties, species and occasionally genera. In principle it can also occur at higher taxonomic grades and there is substantial evidence that this has happened in the deep past. Mitochondria and plastids, for example, may be relics of an ancient commensalism and the lichens evolved as a commensal relationship between fungi and algae—a reticulation event between members of discrete taxonomic classes.

The evidence for natural reticulate evolution has been growing for several decades (see, for example, Arnold, 2009; Arnold & Meyer, 2006; Baroni et al., 2005; Bullini, 1994). Genes from viruses can be incorporated into animal genomes, which would represent a reticulate event linking separate taxonomic kingdoms (Keeling & Palmer, 2008). The evolution of modern wheat, as any archaeologist can testify, is a complex story of polyploidy and hybridization, sometimes across genera (Harlan et al., 1973). Reticulate evolution, then, is a biological fact that can be linked to a number of well-known mechanisms (see Table 1).

The central thesis of this paper is that the hierarchic model represents a ''special'' (rather than general) theory of evolution. In palaeoanthropology, where it has already been suggested that current conceptions of evolution are either unhelpfully out-of-date (Cartmill, 1990; Tattersall, 2000) or incomplete (Foley, 2001), this deep embedding of hierarchical thinking means that more plausible reticulated models may not be receiving the attention they merit.

Great ape (including human) evolution probably followed a stick-slip, saltatory trajectory, punctuated with demographic bottlenecks, convergence, divergence and hybridization events (see Arnold, 2009; Osada & Wu, 2005; and references therein). The use of a non-hierarchic model in these complex situations may create opportunities for increased integration between the human sciences, primatology and palaeoanthropology, which would benefit all. Human affairs are clearly shaped by learned behaviours, purposeful action, chance and choice. Research on other great ape species suggests that they too are *agents*, capable of negotiating new ways of being fit (as work on their cognition and behavioural flexibility demonstrates, see for example Lonsdorf et al., 2010; Russon & Begun, 2004). Among primates, agency influences demographic behaviour and demographic behaviour can sometimes alter patterns of gene flow. These demographic ''hot-spots''

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Table 1. Processes that produce reticulating evolutionary patterns.

Process	Definition
Hybridization	Reproduction across taxon boundaries, for example in the *Papio* baboons (Zinner et al., 2011).
Allopolyploidy	Reproduction across taxon boundaries in which the offspring is *polyploid*, i.e. receives more than the normal number of sets of chromosomes (Doyle et al., 2008). Many plants show polyploidy, including wheat and other cereals used by humans (Harlan et al., 1973).
Lateral/horizontal gene transfer	The direct transfer of genetic material from one organism to another, the most well-known examples of which are the integration of mitochondria and plastids into eukaryotic cells (Keeling & Palmer, 2008).
Incomplete lineage sorting	A process whereby founder effects and the differential loss of alleles in descendent species produces discordant phylogenies when different alleles are studied (Maddison & Knowles, 2006). Incomplete lineage sorting seems to have occurred among the great apes while the genera were diverging (Hobolth et al., 2011).

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create new possibility spaces for future evolution that cannot be understood in a strictly hierarchic frame of reference.

An appreciation of reticulation may give important insights into human evolution. Not all the mechanisms listed in Table 1 create patterns that can be confirmed in the fossil record or laboratory, so this paper will focus primarily on hybridization. With a few exceptions (notably, Arnold, 2009), the idea that reticulation might have not been aberrant but in fact typical, generative and significant in human history has been ignored, even though there is an extensive literature on reticulation in other mammals, plants and insects and much theoretical work has been done (Barton, 2001). In this paper, we first make the case, through a review of the evidence, for considering reticulate evolution as a significant and creative force in the human past and then explore the implications for anthropology and human science of a shift towards a heterarchic view of evolution. We aim to show that there is now sufficient evidence that reticulation has played an important role in the histories of primates and hominins to justify the effort involved in re-thinking our models and assumptions.

The evidence for reticulation among humans and comparable primate lineages

Direct evidence for hominin reticulation comes from morphological and genetic data from humans, our closest living relatives (the nonhuman apes and other primates) and fossil species. Nuclear genetic information is available for two extinct hominins: the Neanderthals, for which we have DNA from a number of fossils dating to 38–70 ka (thousands of years ago) (Green et al., 2006, 2010) and the Denisovan hominin, which dates to 30–50 ka (Reich et al., 2010). Mitochondrial DNA has recently been recovered from a ~400 ka femur from Sima de los Huesos, which may represent *Homo heidelbergensis* (Meyer et al., 2014). For other extinct species, we must rely on the pattern of the fossil record and arguments from anatomical evidence, although interpreting this type of data is much harder.

In addition, we can argue for reticulation in the hominins based on indirect evidence from comparable primate lineages, in which hybridization can be observed directly. Gene flow across taxon boundaries (particularly, although not exclusively, between closely related species or sub-species) is common among the primates (Arnold, 2009), and fuels debate about primate taxonomy. There are two primate groups that are regularly used as comparators for studies of human evolution: (1) the papionins, which have been identified as a rich source of potential analogies for early hominin evolution (Elton, 2006; Jolly, 1970, 2001; Winder, 2012) and (2) the non-human apes, our closest living relatives. This section explores the comparative evidence first and then moves on to the direct data.

It is worth noting that, where both genetic and morphological information exists for a specific group of hybridizing individuals, the signatures of reticulation from one dataset do not always map neatly onto those from the other. Different data-sets may support differing evolutionary reconstructions. Early palaeoanthropological research perforce emphasized morphological regularities. Over the last 30–40 years, however, genetic evidence has become available that has led some scientists to suggest that, where differences arise between morphology and genetics, inferences from genetics must be ''right'' and the anatomical evidence ''wrong''. In studies of reticulation, however, dissonance between signals—whether from different *types* of evidence or different data from the same type (different chromosomes or parts of a chromosome, for example)—is a valuable source of information about the evolutionary process. In this paper, therefore, we have considered both morphological and genetic information. The data should be read with the proviso that *any* single argument has its own uncertainties; just as morphological patterns might be ''wrong'' because of convergent evolution, so genetic patterns might be ''wrong'' because of genetic drift, hybridization, isolation events and rapid radiations.

Reticulation among papionins and hominoids

The papionins comprise seven genera: the common baboons (*Papio*), mandrills and drills (*Mandrillus*), white-eyelid mangabeys (*Cercocebus*), crested mangabeys (*Lophocebus*), geladas (*Theropithecus*), macaques (*Macaca*) and highland mangabeys or kipunjis (*Rungwecebus*) (Davenport et al., 2006; Groves, 2001; Jones et al., 2005). They are thought to be good analogues for the early hominins for several reasons. First, they are (relatively) large-bodied and large-brained, with the mandrill the largest of all living monkeys (Smith & Jungers, 1997). The papionins are also highly social—as we believe our ancestors were—and several genera are terrestrial or semi-terrestrial (Barrett & Henzi, 2008), making them of particular interest to those interested in our adaptations to life on the ground. The common baboons and macaques are also

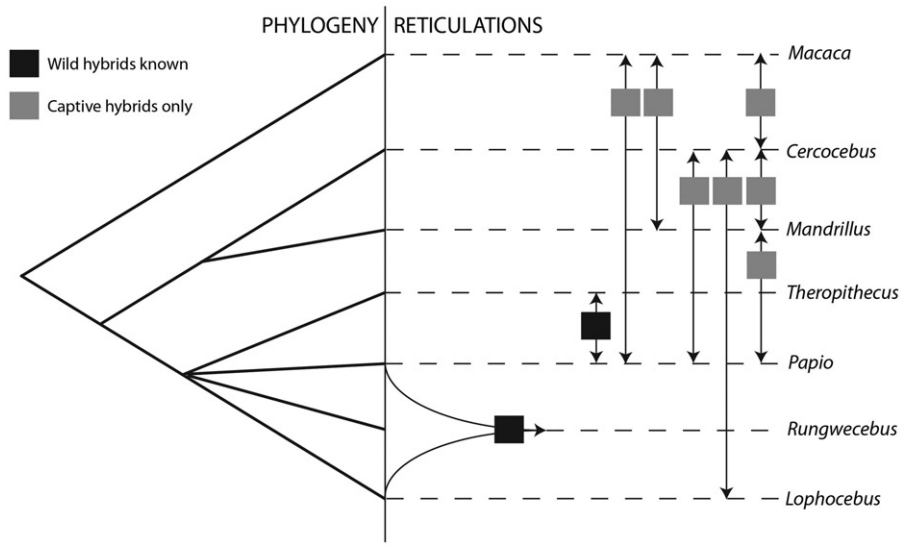

Figure 2. The basic phylogeny of the extant papionins, adapted from Gilbert (2013), together with known reticulations between genera in the wild (Burrell et al., 2009; Dunbar & Dunbar, 1974) and in captivity (Chiarelli, 1973; Craft, 1938; Hill, 1974; Markarjan et al., 1974; Ngugi, 2003; Van Gelder, 1977).

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two of the most widely-distributed and ecologically flexible primate genera, after our own (Abegg & Thierry, 2002; Jolly, 2001) and the radiating evolutionary patterns found among the papionins may reflect similar evolutionary processes to those seen in the hominin fossil record (Jolly, 2001). It is this latter suggestion which makes this group of particular interest here.

Beginning at the inter-genus level, there is a lot of evidence for reticulate evolution among the papionins (Figure 2). Intergeneric hybrids usually occur in captivity and vary in lifespan and fertility status (see, for example, Chiarelli, 1973). The newly discovered kipunji, however, is ecologically and morphologically very close to the crested mangabeys (and was originally placed in the same genus (Jones et al., 2005)), but analyses of its mitochondrial DNA show that the picture is more complex. In fact, there are two populations of kipunjis, in the Southern Highlands and Ndundulu areas of Tanzania, and their mtDNA is different. The mtDNA of the Southern Highlands specimens nests within that of *Papio* (Burrell et al., 2009), while the Ndundulu specimens—which probably retain the original kipunji mtDNA—form a sister lineage to this *Papio-Rungwecebus* clade (Roberts et al., 2010). This suggests that introgressive hybridization has occurred in at least the Southern Highlands kipunji population, presumably involving female baboons and male mangabeys (Zinner et al., 2011). There have also been reports of wild hybrids between the common baboons (particularly olive baboons) and geladas (Dunbar & Dunbar, 1974; Jolly et al., 1997). Hybrids between these latter genera are widely known in captivity and some are long-lived and fertile, although both viability and fertility vary among first- and second-generation hybrids (Jolly et al., 1997; Markarjan et al., 1974).

Figure 2 suggests that some papionins hybridize in captivity more often than others. Nothing is known about the inter-breeding potential of the kipunji from captivity, as it has not knowingly been kept. However, captive geladas are known to have inter-bred with members of one other genus, crested mangabeys with two, mandrills/drills and macaques with three each, white-eyelid mangabeys with four and common baboons with all five. Whether this relates more to the reproductive compatibility of each genus with others, their relative geographic distributions and evolutionary interactions or simply their abundance and history in captivity (which may determine the opportunities a group has for hybridization) is still unclear. It is also not apparent whether inter-genus hybridization occurs regularly enough, especially in nature, to exert a significant effect on primate evolution—although it is worth noting that, thanks to the non-linearity of cause and effect so typical of complex biological systems, any given influence need not be common to be significant and potentially generative. Exploring the significance of rare events for Earth System dynamics is a major topic for scientists today, as for example in the widespread study of mass extinction events in the history of life (Barnosky et al., 2011).

The papionins—especially macaques and common baboons—also hybridize within genera. The common baboons, the most widely-used analogies for early hominins, actually comprise a suite of six major allotaxa, whose taxonomic status and relationships are still uncertain (Zinner et al., 2009, 2013). Common baboon genetic organization seems to follow geographic patterns rather than fitting with the traditional, morphological taxon distinctions (Zinner et al., 2013). All six allotaxa hybridize readily in captivity and in the wild there are substantial, self-sustaining hybrid zones between olive and hamadryas baboons in Ethiopia (Phillips-Conroy & Jolly, 1986) and olive and yellow baboons in Kenya/Tanzania (Alberts & Altmann, 2001). Many baboon hybrids can be identified either from their genomes or their external morphology. In the olive/yellow hybrid zone near Amboseli, Kenya, for example, researchers have identified a phenotypic range from the ''pure yellow'' form to the ''pure olive'', with various intermediates (Alberts & Altmann, 2001). Hybrid individuals are not yet well known in other areas where baboon allotaxa meet in the wild, although they may remain to be discovered.

The macaques also provide clear evidence of reticulate evolution. There are natural hybrid zones in many places where macaque species meet in the wild, and particularly large numbers of hybrids occur between Assam and crab-eating macaques in South-East Asia, between crab-eating and rhesus macaques in the same area and between rhesus and

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Japanese macaques in the Kowloon Peninsula (McCarthy, No Date). Smaller hybrid zones are also well-known. In Sumatra, for example, there are at least six macaque species forming a continuum of reticulating forms; at every boundary where two species meet there is natural hybridization, identifiable both genetically and morphologically (Ciani et al., 1989; Watanabe et al., 1991). There is also some evidence for the existence of hybrid macaque taxa. The stump-tailed macaque, for instance, seems to fit within the *sinica* group in terms of its Y-chromosome DNA and the *fascicularis* group for its mtDNA, suggesting an ancient origin as a hybrid between these two lineages (Tosi et al., 2003). A second group, the Togean macaques, may have their origin in ongoing hybridization between Tonkean and Moor macaques in Sulawesi (Brandon-Jones et al., 2004), although the specific status of this group remains uncertain (Brandon-Jones et al., 2004; Lowe, 2004).

As an alternative to focusing on the papionins as potentially analogous to the hominins, we can also explore the impact of reticulation among humans' closest living relatives, the apes. There is one key difference here, though—while all the papionins have the same number of chromosomes (42; Markarjan et al., 1974), the apes do not all share the same karyotype. Humans have reduced their chromosome number to 46 from the 48 of the great ape group (Ferguson-Smith & Trifonov, 2007), while the gibbon and siamang genera (originally classed as sub-genera) each have different chromosome numbers: 38 in *Hoolock* (called *Bunopithecus* in older sub-genus schemes), 44 in *Hylobates*, 50 in *Symphalangus* and 52 in *Nomascus* (Geissmann, 1995). This makes inter-generic hybridization among these forms less likely, as offspring will tend to have reduced viability and fertility.

There is evidence of inter-specific hybridization among the gibbons. Among the hylobatids, for example, Geissmann (1995) describes natural hybrid zones between *Hylobates lar* and *H. pileatus* in Thailand; *H. agilis* and *H. lar* in peninsular Malaysia; and *H. agilis* and *H. muelleri* in Kalimantan (where there is a large and stable hybrid population). A smaller hybrid zone may also occur between *Nomascus gabriellae* and *N. leucogenys siki* in southern Vietnam and Laos, as evidenced by the apparently hybrid songs sung by gibbons in this area, and the presence of museum specimens whose morphologies are either intermediate or fail to match species attributions based on groups' characteristic vocalizations (Geissmann, 1995). It is worth noting in these examples that recent estimates of gibbon divergence dates suggest all wild hybrids occur between relatively closely-related species. Israfil et al. (2011) give a date of 3.1–4.0 Ma for the divergence between *H. pileatus* and the rest of *Hylobates*, then suggest that *H. lar* branched off from the remaining taxa at 3.3–2.5 Ma and *H. agilis* from *H. muelleri* at 2.9–2.1 Ma. The split between *N. gabriellae* and the *N. leucogenys* clade may have occurred as late as 1.6–1.0 Ma (Israfil et al., 2011). Even with these new divergence dates, however, there is still at least ~1 Ma separating each pair of hybridizing taxa, and some may span gaps of up to 4 Ma. The time-depth of the genus *Homo*, in contrast, seems to be, at most, some 2.5 Ma (Kimbel, 2009), while the australopith radiation, if we include *Paranthropus* but not *Ardipithecus*, dates to between ~4.2 Ma (at Kanapoi, Ward et al., 2013) and ~0.6 Ma (at Swartkrans Member 3, Herries et al., 2009). Even if we interpret this gibbon evidence as demonstrating that reticulation is more likely among closely-related taxa than distant ones, the time spans over which hybridization remains possible in gibbons are comparable to the timescales of hominin evolution. Although we cannot say with certainty that any given group of contemporaneous hominins (like the australopiths) formed a single monophyletic clade, it still seems likely that some closely-related pairs of hominin taxa would have been able to hybridize for long periods and might, in fact, never have become completely isolated from one another. Similar evidence for slowly accumulating reproductive isolation in the mammals has already suggested that *H. sapiens* and *H. neanderthalensis* would have remained capable of producing viable, fertile hybrids until the latter went extinct (Holliday, 2007).

Surveys of zoo gibbons in the 1980s suggested that at least 4% were definitely hybrids and the real number is probably higher (Geissmann, 1995). A possible hybrid between *Hylobates agilis* and *Hoolock hoolock* has been reported in captivity, although the identity of the hoolock parent is uncertain (Montagu, 1950). There is also a relatively well-known case of the two ''siabons'' born in captivity in the 1970s, inter-generic hybrids between *Symphalangus syndactylus* and *Hylobates muelleri*. One of these individuals died young of an unrelated illness, but the other grew to adulthood with 47 chromosomes, 22 from the gibbon parent and 25 from the siamang (Myers & Shafer, 1979). Overall, she showed little chromosomal homology with either parent, suggesting a very complex developmental process which probably made her infertile (Myers & Shafer, 1979). Both siabons showed hybrid genomes and morphologies (combining traits from both parents) and the older one also displayed behavioural traits linked to her hybrid status—vocalizations which were deeper than those of gibbons but lacking the variety of siamangs (Myers & Shafer, 1979). More recently, two hybrids between *Hylobates lar* and *Nomascus leucogenys* were described, the longer-living of which had mixed pelage, a 48-chromosome karyotype (22 chromosomes from one parent, 26 from the other) and other hybrid traits (Hirai et al., 2007). A similar hybrid of *Hylobates pileatus* and *Nomascus concolor* was reported from a US zoo in 1968 (Hirai et al., 2007).

There are no inter-generic hybrids among the great apes, but hybridizations between species or sub-species are relatively common, especially in captivity. Cocks (2007) suggested that 15% of a large sample of captive orang-utans were hybrids, for example, although these individuals—whether naturally or as a result of differential treatment by humans—had lower survival rates than members of either parent species. The two orang-utan species are separated in the wild; however, so do not produce wild hybrids and the fertility of captive ones is hard to assess (Courtenay et al., 1988). Among gorillas, there is genetic and morphological evidence for recent reticulations between sub-species and species in the wild (Ackermann & Bishop, 2010). Studies of morphological traits, including dental and sutural abnormalities often associated with hybrid individuals, suggest that the eastern lowland gorilla population may represent a zone of

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introgression between eastern and western gorillas, while among western gorillas there is a patchy distribution of hybrid anatomies and genotypes which seems to indicate a history of vicariance-driven structuring and admixture as rivers came and went and populations expanded and contracted into refugia (Ackermann & Bishop, 2010). This evidence, therefore, points to substantial recent gene-flow between different populations, sub-species and species of gorilla and to a complex history for the gorilla genus (Ackermann & Bishop, 2010) and this inference is strengthened by the fact that the signals of hybridization appear in multiple different datasets. For chimpanzees and bonobos, meanwhile, which also have non-overlapping wild distributions, Vervaecke et al. (2004) describe four bonobo–chimpanzee hybrids in captivity, each of which displayed a (differing) mixture of morphological traits and had intermediate vocalizations. There is also some evidence for hybridization between common chimpanzee subspecies in captivity, although this does not seem to be common in the wild (Becquet et al., 2007).

Evidence for reticulation among the hominins

The evidence above suggests that reticulate evolution may be common, creative and significant in the histories of both our closest living relatives and the species we believe to offer a good analogy for our early ancestors. However, is the inference of an important role for reticulation among the hominins supported by more direct evidence?

Genetic data from Pleistocene hominin fossils (including Neanderthals, Denisovans and the Sima de los Huesos fossil) seem to support reticulate evolution. The publication of the Neanderthal genome, for example, suggested that 1–4% of the non-African human genome might originate with Neanderthals, although these genes might also represent DNA surviving from the common ancestor of both species (Green et al., 2006, 2010). At about the same time, a genome from a few fragmentary fossils from a Siberian cave suggested the co-existence of a third hominin—the Denisovans—that was as distinct from Neanderthals and humans as they are from one another (Reich et al., 2010). Denisovans apparently contributed 4–6% of the Melanesian human genome, a signal of reticulation that is seemingly more localized but still significant (Reich et al., 2010). There is also some evidence that the Denisovans themselves may have obtained somewhere between 0.5–8% of their genetic material from an unknown archaic hominin with a relatively deep divergence (0.9–4 Ma) from modern humans (Prufer et al., 2014). Finally, the possible *Homo heidelbergensis* mtDNA from Sima de los Huesos is closely related to that of the Denisovans (Meyer et al., 2014). Whatever the explanation for this pattern, it also suggests that the boundaries between populations (and apparently species) in Pleistocene Eurasia were complex and highlights the remaining uncertainty regarding the relationships between morphology and genetic phylogenies (Meyer et al., 2014). All this evidence together suggests that, for recent hominins at least, species boundaries were open and genetic interactions across these boundaries not unusual. Again, it is worth stressing here that just because these amounts (up to ~8% of the genome) may *feel* small, their importance to the functioning of the rest of the evolutionary system may be significant because of nonlinear relationships between causes and effects.

In addition, the genetic and morphological structure of *Homo sapiens* itself, patterned, as it is, into clusters, once called ''races'', now described as ''ethnic groups'', is comparable to the situation among common baboons, which hybridize freely at the sub-genus level and are often described as one widespread species with a number of distinctive subgroups—just like humans. Our ethnic groups, until very recently at least, would have comprised populations that interbred with one another much more often than with members of other groups, but are nonetheless fully inter-fertile provided any cultural barriers (taboos, differences in marriage systems or customs and behavioural norms that might otherwise prevent mixing) can be overcome. Evidence that these ethnic groups—or populations within them—have partially separate phylogenies can be seen in the many modern genetic datasets that separate out different ethnic groups as clusters (see, for example, the classic study of mtDNA by Cann & Wilson, 1992). Their genetic differences could only have been maintained through partial genetic isolation, although it is clear that this is not down to biological incompatibility but, presumably, to geographic and cultural factors.

Reticulating patterns often occur below species level like this, especially in organisms capable of acquiring complex, socially learned behaviours. These behaviours (often described collectively as *agency*) can create behavioural obstacles to gene-flow that disappear when individuals become isolated or socially constructed norms are forgotten. We will return to this topic below. It is sufficient here to observe that the intra-species structure of *H. sapiens* looks like a microcosm of the reticulations visible at higher taxonomic levels in other primates and, according to the evidence above, that same structure probably extended beyond our current species boundaries when our close relatives were still alive. This has already been suggested for the group of taxa close to the origins of *H. sapiens* as part of the multi-regional theory of modern human origins, often mistaken as a model requiring multiple origins rather than a reticulating scheme (Wolpoff et al., 2000).

Reticulation appears to be an important force in the evolution of the primates, up to and including the apes, and again between later members of *Homo*. What happens in between? For most fossils, including all those older than, at maximum, ~400 ka, we have no genetic data (and the oldest nuclear DNA dates to ~70 ka). However, the fossil record is still indicative of possible reticulations. Among the Pleistocene fossil record in particular are several putative hybrid fossils identified on the basis of their morphology. The Lagar Velho child, for example, who comes from a Portuguese cave burial dating to ~24.5 ka, seems to possess a morphology which mixes traits associated with European early modern humans and with Neanderthals (Duarte et al., 1999). In particular, Lagar Velho 1 is human-like in its dental size and proportions and features of the mandible, forearm and pelvis, but similar to Neanderthals in body proportions and muscle insertion patterns (Duarte et al., 1999). The hybrid status of this individual has been challenged, however, on the basis that this argument rests heavily on reconstructed features—like limb proportions—which may be inaccurate

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both because the skeleton is a juvenile and because of taphonomic changes, and in any case do not seem to be reliable discriminators of members of different Pleistocene populations (Tattersall & Schwartz, 1999).

In addition to Lagar Velho 1, fossils from the Pestera Muierii in Romania, which date to ~30 ka, are also identified as hybrids on the basis of their mixing modern human and Neanderthal features, as, indeed, do the anatomies of many other early Upper Palaeolithic fossils (see Soficaru et al., 2006 and references therein). In fact, as Lubenow (2000) notes, there are actually no fewer than 25 ''advanced'' Neanderthals and some 107 ''archaic modern'' specimens, of which any (or all) might be explained by reticulate evolution. It is worth noting, however, that there is no *necessary* link between hybrid genotypes and ''intermediate'' phenotypes, as the discussion of the non-human primates above indicated. Suggestions that specific fossils are hybrids are, therefore, always uncertain. It has also been suggested that it is not intermediate morphology *per se*, but a higher-than-expected prevalence of non-metric trait variation that is most indicative of hybridization in the primates (Ackermann, 2010). Such patterns have not been assessed for early hominins but are found among the Neanderthals, particularly at Krapina, Skhul and Qafzeh (Ackermann, 2010).

Earlier in the fossil record, where there are fewer fossils overall, identifications of putative ''hybrid'' specimens peter out, but we can still see evidence that might indicate reticulation. This evidence comes from two main sources. First, and more generally, the Plio-Pleistocene fossil record shows the hominins as evolving through a series of adaptive radiations (Foley, 2002; Wells & Stock, 2007). An adaptive radiation involves the rapid diversification of a single ancestral form into an array of species, a stick-slip pattern of evolution that contrasts radiations with the periods of ''normal'' evolutionary history between them (Schluter, 2000). While under a hierarchic model of evolution, the products of such a radiation are often presumed to remain separate, it actually seems logical that species which had only recently diverged might remain in contact with one another (subject, of course, to geographic and temporal constraints) and be able to exchange genes for at least some period after their split, just as is the case with the gibbon and common baboon radiations today. We noted in the introduction that stick-slip evolutionary dynamics produce a spatiotemporal mosaic of varieties, species and genera that is particularly conducive to reticulation and, in fact, very recent work on the morphology and evolution of early *Homo* suggests just such an interpretation of the genus' early diversity (Lordkipanidze et al., 2013).

In addition to the evidence of punctuated evolution, radiations and rich, complex suites of hominins present at the large scale, the Plio-Pleistocene fossil record also offers evidence from morphology. As this record improves, it has become clear that there are actually very few characters in the fossil record that show simple evolutionary patterns—instead, many come and go, appearing in different combinations in different places and at different times and changing at different rates (the anatomies of the hand and foot of *Australopithecus sediba*, for example, are described as unique combinations of primitive and derived traits, Kivell et al., 2011; Zipfel et al., 2011). This ''mosaic'' appearance of traits in the fossil record has traditionally been used to promote or deny particular fossils' affinities to modern humans and to push specimens onto and off the direct line to us, but may in fact imply a reticulating lineage exploring a complex, multi-dimensional space of possible morphologies and repeatedly generating and re-generating new combinations of traits. This pattern is, therefore, also compatible with, and arguably suggestive of, an important role for reticulation in hominin evolution. The taxonomic implications of this evidence have not been worked out at the time of writing and substantial research investment will be required to incorporate the possibility of reticulation into systematic practice.

Discussion: Space, time and paradigms in human evolution

Palaeoanthropological research depends on an ontology that remains more or less stable over a deep time perspective. That ontology includes categories of thing (mitochondria, for example, chromosomes and alleles) and some taxonomic categories. If these mission-critical categories too unstable, evolutionary research would be compromised by arguments about shifting boundaries, continuity and change. Some taxa and/or categories may appear more stable than others—the order Primates, for example, is a deep-time construct. On shorter time scales, the hominins and our own species, *Homo sapiens*, may also be treated as stable.

When specimens are discovered that seem to undermine these mission-critical boundary judgements (as, for example, *Sahelanthropus tchadensis* and *Orrorrin tugenensis* do for the hominin clade), scientific disciplines will often allow those categories to become fuzzy. Anthropology is too valuable an enterprise to become bogged down in logic-chopping arguments about boundary-judgements. Scientists learn to live with constructive ambiguity and a palpable mismatch develops between theory and empirical evidence. Different sub-disciplines have different space-time perspectives, ontologies and mission-critical boundaries. When these different disciplines work together, each may find it difficult to accommodate the ontological fuzziness of the others' mission-critical boundaries.

The model of a ''paradigm-shift'' so often presented in the popular science literature, where one paradigm replaces another, is an over-simplification of Kuhn's (1962) hypothesis. What tends to happen is that the established perspective ceases to be a general theory and becomes a special sub-domain of a richer whole. Plate tectonics, for example, did not destroy the foundations of geo-physics, it re-adjusted mission-critical boundaries to accommodate a mass of empirical evidence about continental drift that had been vetoed as ''unscientific'' for decades. Sometimes extensive debate about mission-critical boundaries is a prelude to a paradigm shift, especially when those debates become embedded in a discipline.

Reticulate evolution begs a number of boundary-questions about definitions and categories in palaeoanthropology. If gene-exchange is possible across species boundaries, does this mean that the species concept is meaningless? How much gene-flow is sufficient to undermine the conventional

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hierarchic model? Are terms like species (Darwin, 1859; Wilkins, 2009) or organism (Pepper & Herron, 2008) biologically meaningful, given the persistent lack of a consensus-definition?

In the life sciences, solutions to these boundary problems are artefacts of spatial, temporal and analytical perspective, shaped by an overlay of conventional wisdom and culturally embedded knowledge that protects mission-critical concepts. Different ways of looking at a problem-domain bring different aspects of the evidence to the foreground and background other features. When disciplinary communities work together these perspectives generate predictable patterns of conflict and co-operation that require careful management (Winder & Winder, 2013). Viewed macroscopically, for example, it is almost self-evident that a great ape is a well-bounded organism. We may know, at an intellectual level, that its cells arose through a persistent commensal relationship between at least two, distinctive, prokaryotic forms, that genetic material can be moved across its boundaries by viruses and that microbial cells probably outnumber eukaryotic cells in its body, but this knowledge is backgrounded at the macroscopic level. The species and organism concepts are thereby brought into the foreground and the counter-evidence set aside.

In reflexive disciplines like anthropology there are often wider, societal and ethical dimensions to the paradigmatic veto. If we were to background the evidence of cultural anthropology and foreground the evidence of physiological and genetic research, for example, it would be obvious that anatomically modern humans form a well-defined, interfertile taxon. Ethnically defined sub-taxa, although persistent and stable, are the synergetic upshot of geographical pattern and countless micro-scale demographic events constrained by social norms and regulation. They are related, in a complex way, to culturally embedded beliefs, habits and social learning at a lower level of organization and top-down, institutional constraints. To suggest that the species as a whole may be polyphyletic and that different ethnic groups might have different phylogenies would remind many of the racist anthropologies of the 19th and early 20th centuries and raise challenging ethical questions.

Similar, although much stronger taboos prevent gene-flow between humans and other great apes. If that consensus changed, for example in response to a catastrophic pandemic or commercial pressure, species boundaries would probably change with it. The ethical dimension of the boundary judgement is clear and immediate in this second example because the taboos that limit gene-flow between species are rigidly monitored and regulated by law. In this context, scientific evidence that suggests similar lateral gene-flows may have occurred in the past and could possibly occur in the future might be seen as distasteful or politically tendentious. The reflexive sciences are always ethically challenging.

The reticulation hypothesis is empirically refutable. If it were shown that the fossil and genetic data, processed in different combinations, using different association methods, optimality criteria and linking algorithms, produced broadly similar cladograms, then the reticulation hypothesis could safely be refuted. However, the fossil evidence suggests a mosaic of characters defining a possibility space of hominin development that has been explored by a reticulate lineage of divergent and convergent forms. The Dmanisi hominin assemblage may provide a good example of this.

Recent work by Lordkipanidze et al. (2013) on the Dmanisi fossil skulls suggests there was just one lineage of hominins at the time of *Homo erectus*, some 1.8 million years ago, which may include those fossils previously classified as *H. habilis* and *H. rudolfensis*, as well as the Georgian sample, *H. erectus* and African *H. ergaster*. More interesting than the widely-recognized implications of this for taxonomy, however, is the question of what this means in practice for the evolutionary process and the ways we reconstruct it. Lordkipanidze et al. (2013) suggest a similarity between the demic structures of *H. sapiens* and *H. erectus*, for example, and seem to favour an assumption of genetic continuity between Africa and Eurasia at 1.8 Mya.

The Dmanisi sample could easily be interpreted in a reticulate frame of reference, treating the assemblage as a spatially and temporally discontinuous grab-sample of a widely distributed, polyphyletic lineage which might span one or several ''species'', depending on the species concept used (see Figures 3–5). That lineage's total population and composition would have varied as demes came into contact and diverged again. The frequency and impacts of changes in effective population size would be critical factors in its subsequent history. Mating systems would be shaped by colonization—when demes become isolated by colonizing a new area—and by bottlenecks where populations crash catastrophically and then recover. Either would lead to founder effects, genetic drift and unpredictable compositional variations in the populations that could cause rapid and stochastic evolutionary change. Normal behavioural constraints on outbreeding would be relaxed as new patterns of opportunity and threat were encountered and new co-operative strategies were explored. Low levels of competition might allow poorly-adapted and disabled individuals to survive and reproduce successfully, particularly in populations a little smarter, more compassionate and adaptable than the rest (Winder & Winder, unpublished).

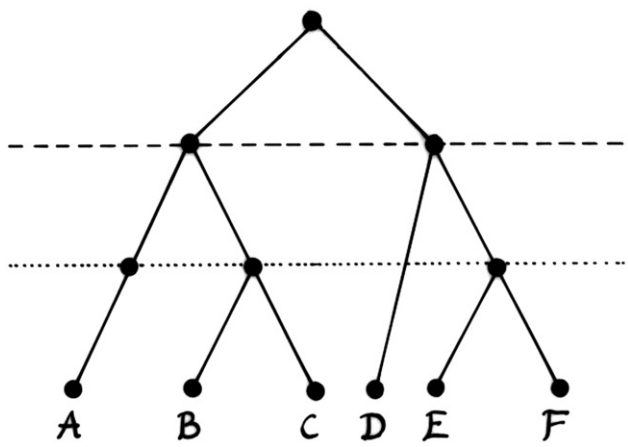

Figure 3. A demographic hierarchy representing the transmission of mitochondrial DNA from mother to daughters. For simplicity the male nodes have been omitted. The hierarchical inheritance pattern manifests as a cascade of one-to-many links. Chromosomal DNA does not follow this pattern.

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The best-known bottlenecks are those associated with the Pleistocene glacial–inter-glacial cycles and related human population expansions and contractions, which we can reconstruct from genetic data (Hawks et al., 2000; Lahr & Foley, 1998). However, accepting a reticulating evolutionary model implies that reductions in the effective (although not necessarily the *potential*) population size may occur much more commonly, as demes move into and out of contact with one another. This is why, under these circumstances, any classification based on the current inter-breeding of demes or their shared morphological traits is unlikely to accurately reflect the recent history of those groups.

Punctuated (stick-slip) evolutionary patterns, as hinted above, are also inter-connected with questions of effective population size and deme/lineage boundaries. An isolated deme, even if it is only temporarily out of contact with others, may display an increased evolutionary rate thanks to founder and bottleneck effects, but will probably stabilize with time. When it reconnects with other demes, however, there is likely to be another surge in evolutionary rates, as the once-separated demes exchange genetic material and produce new combinations of traits and evolution must compensate for ''unforeseen'' effects arising from the mixing of hitherto distinct adaptive complexes. The regularity of changes to the size and composition of parts of a reticulating lineage makes punctuated evolutionary patterns much more likely.

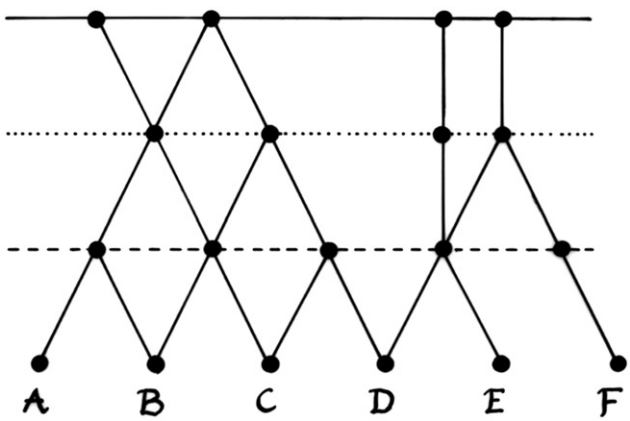

Figure 4. Reticulate evolution. Each node represents a set of organisms; each horizontal slice represents a more or less contemporary assemblage of populations. Patterns of gene flow are represented by edges connecting nodes.

As this discussion has suggested, a reticulating evolutionary pattern ties together stick-slip evolutionary dynamics, changes to population sizes and the changing spatial and temporal configuration of demes in a reticulating lineage. If we envision such a scenario for the hominins, our ability to reconstruct our evolutionary history changes. In particular, it becomes hard to see, under such a model (Figure 5, right), how any molecular clock assumption can be justified. The molecular clock, which assumes roughly uniform rates of genetic change, simply does not work where uniform rates of gradualistic evolution seem so unlikely, populations pass through demographic bottlenecks and hybridization events may be pivotal. While a lot of work has already been done on the use and accuracy of molecular clocks in studies of human and primate evolution (see, for example, Elango et al., 2006; Steiper & Seiffert, 2012; Steiper & Young, 2008) and some new phylogenetic methods that explicitly consider hybridization have been developed (Xu, 2000), it is worth noting that such assumptions still remain key to many genetic studies of people and primates.

If anthropology's molecular clocks are broken, then ''fixed point'' calibration seems less useful. Attempts to reconstruct hierarchic phylogenies, to reconcile the genetic and the fossil evidence for human evolution and to model the processes which might underlie our past depend upon neo-Darwinian assumptions and include some expectation that events are both dateable and (usually) adaptive. Much of the change associated with reticulating events—like founder effects and rapid accommodations to new genetic configurations after the re-connection of previously isolated demes—cannot be explained adaptively. If we can no longer assume an adaptive basis for human biology, for example, does the way we explain and handle the evidence need to change? And if different mating systems, with different demographic structures, might be linked to differing overall rates of evolution, how meaningful are comparisons between distinct societies? Might culture have an effect on deme inter-connectedness through time and space and might hominins, as agents, thus re-shape their own evolutionary history? These questions are brought to the foreground of anthropological research when reticulation is taken seriously, but are pushed into the background by the hierarchic perspective.

The reticulate model is more consistent with the empirical evidence of primate evolution and behavioural ecology than

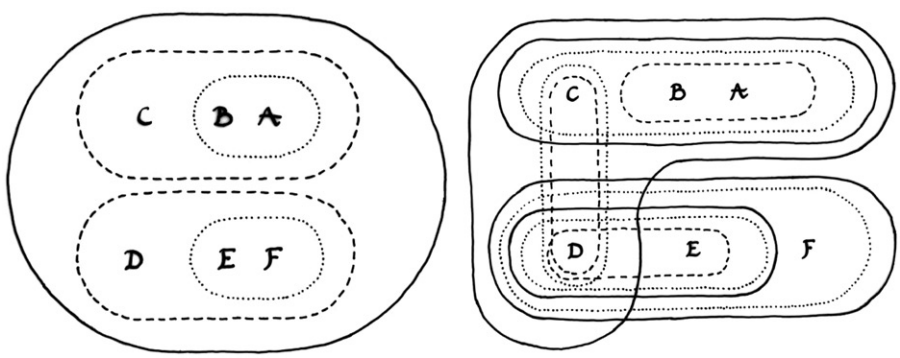

Figure 5. Taxonomies reconstructed from the hierarchic model of Figure 3 on the left and the reticulate model of Figure 4 on the right. The cross-cutting taxonomic boundaries on the right are consistent with the mosaic of morphological attributes described for the *Homo* lineage.

the strictly hierarchic model. Critics who feel justified in dismissing evidence from hybrids in zoos as somehow ''artificial'' must explain in what way these artificial circumstances differ from natural demographic bottlenecks and the chance isolation of small founder populations of closely-related types in marginal territories. They must also explain the mass of evidence that natural hybrids do indeed form, that some well-defined species appear to have hybrid origins, and that the empirical evidence for early *Homo* is more consistent with the mosaic model, locally reversible evolutionary pathways and reticulation.

Whichever aspect of the human biology of the past one chooses to focus on, we would recommend that greater consideration of alternative evolutionary models and particularly the possibility of reticulate evolution would be valuable. We can no longer afford, in light of both the growing evidence from primatology and biology and the potential benefits to our understanding from learning more about these critical aspects of our past, to ignore the possibility of complex, reticulating evolutionary patterns and a greater role for agency. Until we ask the relevant questions, we will never know the answers. By assuming hierarchy, we may be constraining our understanding of the relationships between fossil taxa, their ecological niches and distinctive features and the sorts of biological, environmental and behavioural processes that transformed them.

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Declaration of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

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