

THE LAST COMMON ANCESTOR

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SUMMARY

Humans have no close living relatives and so it is of interest to human ethologists to try and model the characteristics of the last common ancestor (LCA) of humans and chimpanzees. This can be done by examining similarities in the behaviour of these species and also by considering their behavioural differences. This analysis indicates that the LCA was a self-aware, tool-using, hunter-gathering, hand-assisted arboreal biped. It is suggested that the human line's most likely point of origin was in the flooded/swamp forests of what became the Congo basin following the uplifting of the East African Rift region during the mid-to-late Miocene. It is proposed that this subsidence created the conditions for the LCA line to divide based on propensity to engage with water and that this is still reflected in the behaviour of chimpanzees and humans today.

COMMENTARY

Tinbergen's four questions of Form, Function, Ontogeny, Phylogeny, the 'what does it look like, 'what does it do', how does it change within an individual's lifetime', 'how do other closely related species solve homologous problems' questions (Hendrie, 2022, after Tinbergen, 1963) are undoubtedly Ethology's most powerful tools. They provide guidance for systematic study that is missing from disciplines like Psychology and elevate what would otherwise be an interesting technique for analysing behaviour into a scientific discipline.

Whilst answers to the first three questions can be obtained by direct observation, answering questions about phylogeny is less straightforward for those studying humans as there are no close relatives of our species still in existence. Comparisons with chimpanzees (*Pan troglodytes*) are commonly made on the basis of there being a 96% overlap between genomes (The Chimpanzee Sequencing and Analysis Consortium, 2005). Whilst this is clearly of importance for biomedical studies etc, it is of lesser relevance when considering behaviour as behaviour is not predicted by genetic relatedness. There is for example, significant genetic overlap between humans and simple animals like sponges (Gaiti et al, 2017). A significant proportion of the human genome also derives from endogenous retroviruses (Nelson et al, 2003) and other hominins, such as Denisovans/Neanderthals (e.g. Malaspinas et al, 2016) and whilst bonobos (*Pan paniscus*) are

near genetically identical to chimpanzees (Mao et al 2021) their social structures are different and their behaviour differs in several important ways (Gruber & Clay, 2016).

Genetic evidence suggests that the line that led to anatomically modern humans and the line that led to chimpanzees/bonobos started to diverge around 10-12 million years before present (Langergraber et al, 2012) and this and other evidence (Lebedev et al, 2000) indicates that the process of separation was complete in the order of 6-7 million years ago (DeSilva, 2021).

In terms of behaviour, chimpanzees are adept tool-users, and will use a variety of sticks to pestle pound palm hearts, dig for roots/into termite mounds, and to termite 'fish' (Boesch & Boesch, 1990, Sanz et al, 2004). An extension of this termite fishing behaviour is to use sharpened sticks to stab at lesser bushbabies (*Galago senegalensis*) hiding in hollows in trees (Pruetz & Bertolani, 2007). Chimpanzees will also use hammer and anvil stones to crack nuts (Sakura & Matsuzawa, 1991), a behaviour that is at least 4,000 years old and that has been found to leave behind artefacts very similar to Neolithic human-made stone hammering tools (Mercader et al, 2002, 2007). They have also been found to use a complex array of tools for honey extraction (Boesch et al, 2009) meaning chimpanzees are tool set users and not just users of simple tools. The use of stones as tools is of course only one short step away from the evolution of stone tool technology of the sort seen in early hominins (Carvahlo et al, 2009). Other shared behaviours include bedmaking (Koops et al, 2007; Hernandez-Aguilar, 2009), the use of caves for shelter (Pruetz, 2007) and cooperative hunting (Mine et al, 2022). Chimpanzees also ingest medicinal plants (Ohigashi, 1994) and use termite-like insects to bind wounds in self and others (Mascaro et al, 2022).

In terms of cognitive abilities chimpanzees are self-aware, as indicated by the mirror-test (Povinelli et al, 1997), and this is a trait shared by Great Apes but not gibbons or monkeys (Suddendorf & Butler, 2013). Chimpanzees are also able to construct mental representations and to use these to deceive (Whiten & Byrne, 1988). With a sense of self, comes a sense of others and so it comes as no surprise that whilst chimpanzees do not have language in the same way humans do, they have a sophisticated gestural system (Graham & Hobaiter, 2019). This gestural system has overlaps and communalities with the gestural communications of other Great Apes (Byrne et al, 2017) and recent studies have shown that humans are able to understand many of these gestures (Graham & Hobaiter, 2023) indicating a common origin. Together these common behaviours strongly suggest that the last common ancestor (LCA) was a self-aware, tool-using, hunter gatherer and that reflections of these attributes can be seen in all the Great Apes, including humans (McGrew, 2010).

Whilst these similarities are compelling, humans nonetheless have a number of features which make them stand out from the Great Apes, not the least of which being our bipedalism. With this came major anatomical changes, particularly to spine/pelvis (Lovejoy, 2005) and ankles/feet (McNutt et al, 2018) in a move away from the Great Apes hand-like structures to a form that is uniquely our own, with a large heel, stiffened midfoot and greatly strengthened hallux for propulsion, with the other toes shortened. Chimpanzees/bonobos and gorillas (*Gorilla gorilla*) are by contrast knuckle walkers. They arrive at this locomotor strategy through different routes however (Ragni, 2020) and so knuckle-walking in chimpanzees probably developed after the split from the LCA. The LCA itself was most likely to have employed hand-assisted arboreal bipedality, such as seen in modern orangutans (Crompton et al, 2008).

In addition to bipedalism humans have a number of other Great Ape-atypical features including fleshy noses, subcutaneous fat and lack of body hair, and these have led to the suggestion that part of our evolutionary history was spent in close association with water, since these features are rather more typical of marine mammals (Hardy, 1960; Morgan, 1972; Verhaegen, 1985; Kuliukas, 2002, Vanechoutte et al, 2011; Evans, 2019).

There have been a number of objections to this 'Waterside' hypothesis (e.g. Langdon, 1997; Foley & Lahr, 2014; Roberts & Maslin, 2016). However, most of the arguments against are fundamentally in defence of other hypotheses (e.g., Rantala, 2007; Langdon, 2012). One of the

most favoured is the 'Savannah hypothesis' which posits that the transition from 'Ape to Ape-man' (Morris, 1967) took place on the open plains of East Africa, with, for example, adaptations like bipedalism giving a higher vantage point for spotting potential prey (for review see Bender et al, 2012). Humans are not however well adapted for living in such an environment as we have dilute urine and moist dung. We also sweat freely, quickly overheat and die of thirst if we go without water for more than 2-3 days (Morris, 1994).

Other theories along the same lines include the endurance running hypothesis (Bramble & Lieberman, 2004). Humans are well adapted to long distance running and our abilities as persistence hunters are well documented (e.g., Glaub & Hall, 2017). However, the energetic inefficiencies of the intermediate stages of the transition to bipedalism (e.g., Sockol et al, 2007) mean that running for more than a few steps is only really feasible once the adaptations necessary to be fully bipedal have been developed.

Given the inadequacies of the savannah hypothesis and its variants, the Waterside hypothesis remains the most parsimonious when accounting for how our ancestral species came to acquire so many Great Ape-atypical features (Verhaegen et al, 2007). There has been speculation regarding locations where these events may have taken place (e.g. Morgan, 1972; Krill, 2020) but the emerging consensus is that the critical environment was aquariboreal (e.g. Verhaegen et al, 2002, 2007). That is, swamp forest, rather than the beach scenario originally envisaged by Hardy (1960) and we know of course that the period of interest was in the order of 6-10 million years before present.

Importantly, in that context, geological modelling shows that mantle convection drove the uplifting of the East African plateau and that by 15 million years before present the uplift had reached 500m and by 10 million years before present it had reached 1km (Moucha & Forte, 2011). The same modelling reveals subsidence to the west of the East African Rift zone, to form what is now the Congo basin. This subsidence, in combination with the high rainfall in this region, would have led to a marked increase in the area covered by flooded/swamp forest, and this is reflected in the Congo deep sea fan (Anka et al, 2009).

Swamp forest still exists today in the Congo basin and is characterised by high canopies, lush undergrowth, and mud, all of which make moving through them on land very difficult. Travelling through water would have been the easier option in these conditions and this in turn would have provided a strong incentive for the less water averse amongst our LCA to enter the water and so put us on an evolutionary path that eventually led to bipedalism.

Chimpanzees are by contrast more immersion-in-water averse, and in areas where forests seasonally flood, they tend to concentrate into the dry areas in the high-water seasons (Poulsen & Clark, 2004). This behaviour gives a powerful illustration of how important a propensity to engage with water may have been for the splitting of lines from the LCA (Niemitz, 2010). This may also explain the more recent split in the chimpanzee/bonobo line, where the less water averse ancestors of what became bonobos were able to cross the Congo River and exploit the gorilla-free ranges to the south (Hohmann et al, 2019).

Questions about how our ancestral species avoided predation from crocodiles during this period are answered by studies that show man-eating species (*Crocodylus niloticus*) originated in Australasia and do not show up in the African fossil record until 2-3 million years before present (Oaks, 2011). Hence, the LCA's only contact with Crocodylians during this swamp forest phase would have been with slender-snouted fish eaters.

Reasons why our ancestral species left the swamp forest are less clear but may have been to do with the trend towards a cooler/drier climate over the past 4-5 million years (Zachos et al, 2001). This is associated with a shrinkage in the distribution of African forests (Plana, 2004) and so our ancestral species could have thus found themselves in a different environment without having changed location.

This general trend towards cooling has been accompanied by increasingly rapid (in geological terms) fluctuations in temperature and hence environmental conditions and this has been a driver

for Hominin expansion and diversification (Potts, 1998). From an ethological perspective this makes it even more remarkable that behaviours that have come through from the LCA have persisted over all this time in both humans and chimpanzees/bonobos.

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CONFLICTS OF INTEREST

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