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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Not from the apes? Björn Kurtén's views on human evolution

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Herein, I review the Finnish palaeontologist Björn Kurtén's (1924–1988) views on human evolution, as he presented them in his books. In particular, I discuss Kurtén's controversial hypothesis of an ancient, Oligocene separation of the human and great ape evolutionary lineages. This hypothesis, which he argued for strongly in the early 1970s, was based mainly on the idea that the human dentition could not have evolved from an ape-like dentition. Kurtén thought that some of the fossil primates known at the time, especially *Propliopithecus* and *Ramapithecus* from the Oligocene and the Miocene, respectively, were plausible human ancestors because of their supposedly human-like dentitions. New lines of scientific evidence forced Kurtén to abandon his 'not from the apes' hypothesis in the 1980s. However, he continued to speak favourably of other minority views within palaeoanthropology, such as the so-called aquatic ape hypothesis, until the end of his life.

Introduction

The Finnish palaeontologist Björn Kurtén (1924–1988) was a world-famous authority on fossil carnivores. A significant part of his publications dealt with these animals (Werdelin 1992, Pihlström 2010). However, Kurtén was widely interested in other fields of palaeontology, including palaeoanthropology and the study of the human fossil record, and he published a few original research papers on human evolution (e.g. Kurtén 1960, 1971b). He also published several popular books that dealt partly or mainly with human evolution (e.g. Kurtén 1963, 1971a, 1972a, 1972b, 1993). Many of these books were translated into different languages. Kurtén typically wrote the English editions himself, often working simultaneously on a Swedish version of the same book (Leikola 1992). In this review, I refer to the books' English editions (which in some cases have a later publication year than the Swedish original) when such exist.

In his books on human evolution, Kurtén discussed then-current views on the subject. However, he also presented his own opinions and hypotheses, and these were sometimes rather unconventional. Notably, from the late 1960s and almost until the mid-1980s, Kurtén was a proponent of the view that the human and the great ape evolutionary lineages, or the traditional families Hominidae and Pongidae, had separated from each other a very long time ago. He argued that these two families' respective ancestors were identifiable already among

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the Oligocene primates in the famous Egyptian fossil site of Fayum. Furthermore, for many years, Kurtén defended the idea that the primate *Ramapithecus*, known from fragmentary remains found in the Miocene deposits in India, was a direct human ancestor. Kurtén's adherence to an ancient separation of the human lineage also later led him to speak favourably of the so-called 'aquatic ape hypothesis' as a possible explanation for certain biological traits of humans. These ideas were minority views already at the time when Kurtén expressed them in print. Here, I review the development of Kurtén's hypotheses of human evolution as he presented them in his publications, especially the books *Not from the Apes* (Kurtén 1984) and *Our Earliest Ancestors* (Kurtén 1993). I also compare Kurtén's views on this subject with those of other researchers.

Kurtén and the changing views on hominid evolution

Kurtén's intellectual background

From the late 19th century until the Second World War, the main influences on Finnish science, including the geo- and biosciences, came from continental Europe, especially Germany. For decades, Finnish scientists were educated and trained in the German scientific tradition, and their professional publications were mainly in German. In 1924, when Kurtén was born, the German science tradition was still the dominant one in Finland, but while he was growing up, Kurtén himself never felt a strong affinity to it, even though he could read German fluently. In a 1984 interview, he stated that while he was enlisted in the military during the Second World War he taught himself English in part as a protest against the, in his view, excessively pro-German atmosphere in Finland at that time (Hård 1984).

Kurtén's Anglophilia was also evident in his views on biological evolution, which were strongly influenced by American evolutionary biologists. Of special importance were the writings of George Gaylord Simpson (Kurtén 1988, Donner 2014). Simpson was one of the key architects of the 'modern synthesis' and played an integral part in bringing palaeontology into a solidly Darwinian framework (Laporte 2000). Simpson's highly influential mammal classification of 1945 was for decades the standard work on the subject. In this classification, Simpson, an adherent of the school of 'evolutionary systematics', followed the principle that while higher-level taxa, i.e. taxa above the genus level, should share certain characteristics, it was not a requirement that taxa were strictly monophyletic. Thus, Simpson could, and did, accept taxonomic categories that represented 'grades' rather than clades (Hagen 2009). Kurtén would later apply this taxonomic philosophy to his own hypotheses relating to human evolution (*see* below).

When considering Kurtén's views on biological evolution it is also relevant to consider that, for most of his career, he lived and worked in Finland, a country that effectively lacks an indigenous fossil record, and which prior to Kurtén's time had very modest palaeontological traditions (Donner 2014). Before Kurtén, almost the only notable Finnish-born palaeontologist was Alexander von Nordmann (1803–1866), who collected fossils for the University of Helsinki in present-day Ukraine (Moring 1984). These fossils, which included large numbers of remains of the cave bear (*Ursus spelaeus*), would be of great importance to Kurtén, who started his professional career by studying them (e.g. Kurtén 1955, 1957). Partly out of the necessity to be able to access research materials, Kurtén travelled extensively from the very beginnings of his career and visited palaeontological collections in other countries. These visits resulted in many professional links to and personal friendships with colleagues in other countries (Anderson 1992). However, in Kurtén's native country, an active palaeontological community was mostly lacking during his lifetime. Notably, palaeoanthropology was a palaeontological sub-discipline virtually without practitioners in Finland. Kurtén himself, while well-read on the subject, was not a palaeoanthropologist by training, and thus he approached the subject as an outsider. In his writings, Kurtén typically discussed human evolution in the context of Pleistocene mammal evolution in general, rather than, for example, from a more narrow taxonomic or functional morphology viewpoint. This big-picture approach had both advantages and disadvantages; on one hand it could allow

Kurtén to reach insights that more specialist colleagues might miss, but on the other hand it also included the risk of over-generalising.

Early views on the evolutionary relationship between humans and great apes

When Kurtén published his first book on human evolution, *Människans utveckling*, in 1963, the field of literature on human evolution was already about one century old. Famously, Charles Darwin avoided discussing the subject of human evolution in *On the Origin of Species* (1859). However, almost immediately after the publication of Darwin's book, other scientists started forming hypotheses regarding the relatedness of humans to living species, especially to the great apes, i.e. the chimpanzees, gorillas and orangutans, and to the 'lesser apes', i.e. the gibbons. Ernst Haeckel (1868) noted that each of these four different kinds of apes uniquely resembled humans in some respects while differing from humans in other respects. Thus, he did not consider any one of them to be clearly more similar to humans than the others were, although Haeckel did slightly lean towards the view that humans had a closer affinity with the Asian apes. In contrast, both Thomas Henry Huxley and eventually Darwin himself thought that the African apes were morphologically, and therefore by inference phylogenetically, the most similar to humans (or, according to the usage at the time, to 'man'). Huxley (1863: 70) wrote that "It is quite certain that the Ape which most nearly approaches man, in the totality of its organization, is either the Chimpanzee or the Gorilla". Darwin (1871: 199), in turn, wrote that "In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely related to the gorilla and chimpanzee; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere."

Darwin added, however, that at the time of his writing, no primate fossils had yet been found in Africa. In fact, in 1871, the only fossil ape taxon known was *Dryopithecus*, which had been discovered in France in Miocene-age deposits (Lartet 1856). Furthermore, many aspects of the biology of the living ape species were also still relatively poorly known, especially in the case of the gorilla, which had been scientifically discovered only a few decades earlier (Groves 2008).

Traditionally, virtually all researchers agreed that the living great apes formed a natural taxonomic unit, a family called Pongidae, whereas living and extinct humans formed a separate family, Hominidae. This view implied that the orangutan is a close relative of the gorilla and the chimpanzee, and that all living great apes are thus, contra Huxley and Darwin, equally distant relatives of humans. The main disagreement among researchers was on the questions of how distant the ape–human relationship was, and in which part of the world the earliest human ancestors had lived. As for the latter question, most researchers in the early 20th century favoured Asia over Africa as the continent where humans had first evolved. For example, Osborn (1927, 1928) asserted that humans had their origin in central Asia. He also wrote that "pro-man stock was well established in Oligocene time" (Osborn 1928: 154). At the time of Osborn's writing, the Oligocene period was thought to have ended ca. 16 million years ago, rather than ca. 23 million years ago according to modern estimates (*see* http://www.stratigraphy.org/ICSchart/ChronostratChart2022-02.pdf). Osborn was, however, not content with insisting on an early divergence of humans and apes; he was opposed to even calling human ancestors 'apes', thinking that the term should be used for the modern species only (Osborn 1927). Thus, Osborn was possibly the first naturalist in the post-Darwinian era to propose a 'not from the apes' hypothesis of human evolutionary origins (Fig. 1). Instead, Osborn preferred to say that humans had evolved from a 'neutral stock' of primates, and any morphological or other similarities between humans and living great apes were, in his view, the result of convergent evolution.

Other contemporary scientists disagreed with Osborn's extreme opinion of the distinctiveness of the human lineage, while still agreeing that the divergence of the human and ape evolutionary lineages took place a very long time ago. For

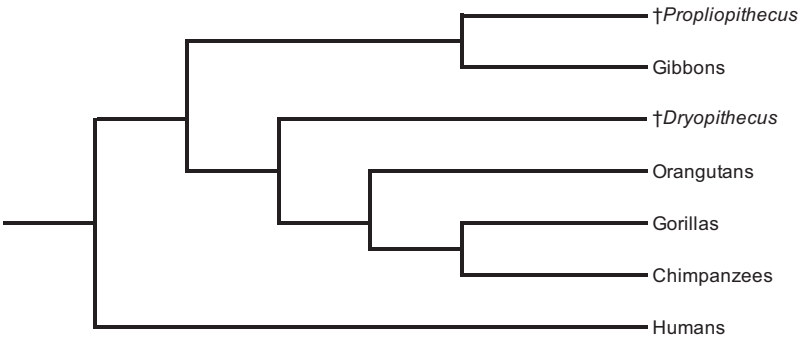

Fig. 1. Phylogenetic relationships of selected fossil and living primates, according to Osborn (1927); † = extinct taxa. In Osborn's view, humans were the sister taxon to all other 'apes'.

example, Gregory (1927a: 395) stated that "[n]o matter how many millions of years ago man and the chimpanzee parted company, the anthropoid apes are still justly regarded as man's nearest relatives among existing mammals", but he also thought that the lineage leading to the great apes separated from the human lineage at the Oligocene–Miocene boundary (Gregory 1927b). Similarly, Keith (1915: 507) argued that "the human and anthropoid lines of descent separated in pre-Miocene times". Until around the early 1960s, most students of human evolution, on both sides of the Atlantic, held similar opinions.

There were, however, observations that did not fit these views. In the early 20th century, biochemical comparisons were suggested by some to be a potential tool for elucidating phylogenetic relationships between animal species. Nuttall (1901) and Grünbaum (1902) performed pioneering experiments with comparisons of blood antisera of different mammals. Their results showed that the similarities between humans and other primate species were of a more complex kind than previously thought. Notably, Grünbaum (1902) found that serologically, humans, chimpanzees, gorillas and orangutans were extremely similar to each other, far more similar than any of them were similar to monkeys. Furthermore, of these four species, it was orangutans, and not humans, that were the most distinct. Taken at face value, these results suggested that the relationship between humans and the great apes, and especially humans and the African great apes, was closer than comparative anatomy suggested.

Most palaeontologists, physical anthropologists and comparative morphologists either downplayed the significance of the blood antiserum studies or ignored them. A notable exception was the German anthropologist Hans Weinert. In the early 1930s, Weinert, a physical anthropologist by training (Schaeuble 1967), combined all data available at the time to form a hypothesis on the relatedness between humans and the great apes. He compared skeletal anatomy, soft tissue anatomy (including gamete morphology) and biochemical characters (blood antiserum studies) of the living species, and reviewed the known fossil record, including the then recently discovered fossil skull of the juvenile *Australopithecus* from Taung, South Africa (Dart 1925). Weinert quantified his results by calculating indexes of relative dimensions of various skeletal parts, and used this information to tabulate similarities between extant and fossil primate taxa. Weinert found that of the living species, the chimpanzee was most similar to humans; the next most human-like species was the gorilla, then the orangutan, then the gibbon (Fig. 2). He thus concluded that among the living species, humans, chimpanzees and gorillas were also the three taxa most closely related to each other; i.e. they formed what modern researchers would call a 'clade'. Weinert called the human–chimpanzee–gorilla group *Summoprimaten*, or the 'summoprimates' (Weinert 1932, 1940). He also estimated phylogenetic divergence events and arrived at results remarkably similar to those accepted today. According to Weinert's estimates, gibbons diverged from the great ape + human lineage in the mid-Oligocene. Next, orangutans diverged from the African ape + human lineage in the late Miocene, and gorillas then diverged from the chimpanzee + human lineage in the mid-Pliocene.

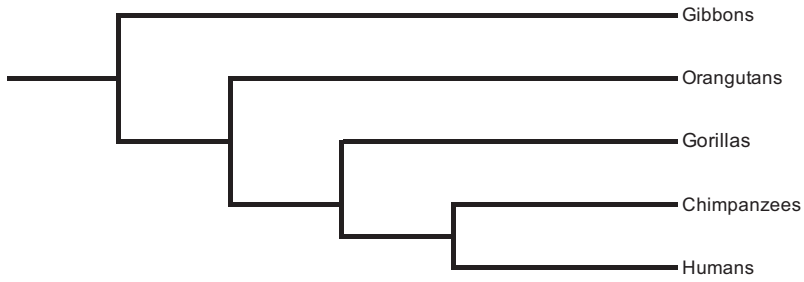

Fig. 2. Phylogenetic relationships of humans and the living apes, including gibbons, according to Weinert (1932). Although he took account of fossil primates, Weinert did not attempt to place extinct taxa into his tree.

Finally, the chimpanzee and human lineages diverged from each other at the end of the Pliocene (Weinert 1932). Weinert's estimates of the lengths of the geological epochs differed somewhat from those accepted today; thus, to Weinert a 'late Pliocene' divergence meant that the event took place as recently as ca. 2 to 3 million years ago. (Weinert's divergence date estimate was much more recent than almost any subsequent estimate has arrived at. However, 30 years later Sherwood Washburn argued for an even more recent divergence date. Mainly based on primate comparative skeletal anatomy, he suggested that the human and ape lineages had diverged only ca. 1 million years ago. According to Washburn (1963: 203), "[m]ost of the characteristics of *Homo* seem to have evolved well within the Pleistocene, and there is no need to postulate an early separation of man and ape".)

Weinert's 'summoprimate' hypothesis was radically different from most of his contemporaries' ideas of the relatedness between humans and great apes. Perhaps unsurprisingly, Weinert's ideas were not widely accepted, or even much discussed, during his lifetime. An exception was the science writer Herbert Wendt, who devoted an entire chapter to Weinert's 'summoprimate' hypothesis in his book on the history of research on human prehistory, *Ich suchte Adam* (Wendt 1953). This German-language book became a best-seller and was translated into several languages, including Swedish (1955). A Swedish edition was found in Kurtén's personal library (my pers. obs.), so it is reasonable to suppose that Kurtén was, via Wendt, at least aware of Weinert's 'summoprimate' hypothesis, even though he never referred to it in his own writings, even to criticize it (*see* below).

Presumed human ancestors in the primate fossil record: the view in the mid-20th century

Aside from a few dissenting opinions such as Weinert's, at the time when Kurtén began his own palaeontological career the majority view was thus that the relatedness between humans and the living great apes was fairly distant. A widely held belief among palaeoanthropologists was the idea that humans are, anatomically speaking, primitive compared to the living great apes. According to this view, most of the then-known fossil apes, such as *Dryopithecus*, were already too anatomically specialised to be possible human ancestors, and therefore the origins of the human lineage should be sought among even older fossil forms (e.g. Straus 1949).

Ever since the early 20th century, some supposedly human-like Oligocene primates from the locality of Fayum, Egypt, have figured prominently in these discussions. One of the earliest Fayum primates to be discovered was *Propliopithecus*. Its fossil remains consisted mainly of teeth and jaws, but students of human evolution noted that its dentition seemed human-like; *Propliopithecus* had, for example, relatively small canine teeth. Based on its dentition, early studies considered *Propliopithecus* a likely ancestor of both humans and apes (Schlosser 1911, Beard 2004). Decades later, Simons (1965), following his studies of the Fayum primates, suggested that *Propliopithecus* might instead have been ancestral only to humans, and not to the living great apes. Thus, the human evolutionary lineage would have been separate from the lineage leading to the apes since the Oligocene, just like Osborn, Gregory, Keith and many others had previously suggested. Later

(1967), Simons retreated slightly from this position by suggesting that *Propliopithecus* and another Fayum primate, *Propliopithecus*' presumed descendant *Aegyptopithecus*, were ancestral forms to both humans and living great apes.

Simons also played a central part in the study of a later-living primate, *Ramapithecus*. This fossil primate, originally discovered in the early 20th century (Pilgrim 1910), was described as a new genus in the 1930s (Lewis 1934). Its initial remains, which were found in Miocene-age deposits in the Siwalik Hills in India, consisted only of a fragmentary right maxilla. However, the shape of the maxilla and the teeth had some seemingly human-like characteristics. For example, rather than having parallel tooth rows like modern great apes, the shape of *Ramapithecus*' dental arcade appeared to be diverging as in humans. Further, although the canine tooth was missing, the alveolus suggested that it had been small and there was essentially no diastema. Due to the fragmentary nature of the fossil material, the phylogenetic affinities of *Ramapithecus* were, however, difficult to ascertain, and for decades, this taxon rarely featured in discussions in the scientific literature. However, in the 1960s Simons and Pilbeam undertook a systematic study of the *Ramapithecus* materials (Simons 1961, 1964, 1968, 1977, Pilbeam & Simons 1965, Pilbeam 1966, 1972). These authors argued strongly for the hominid status of *Ramapithecus*, stating that it was "almost certainly man's forerunner" (Simons 1964: 535). This opinion was soon accepted by most palaeoanthropologists. As for the evolutionary origin of *Ramapithecus* itself, Pilbeam and Simons (1965) suggested that *Ramapithecus* could have evolved either from a dryopithecine, sometime between the early and the middle Miocene, or from a species more like *Propliopithecus*. Interestingly, a careful reading of Pilbeam and Simons (1965) shows that they recognised the possibility that among the extant great apes, the orangutan may, in fact, be more distantly related to humans than the African apes are. They wrote that "Even if *Ramapithecus* and *Pan* had a more recent common ancestor than either did with the orangutan, the Hominidae are presumably definable in terms of [an] adaptive shift" (Pilbeam and Simons 1965: 238). Thus, due to its presumed human-like characters, *Ramapithecus* would still qualify as a human ancestor rather than as an 'ape' according to Pilbeam and Simons. Many other scientists at the time, such as Simpson (1959, 1962, 1963), held similar, grade-based taxonomic views (*see* below).

However, in the early 1960s, new lines of evidence questioned the idea of an ancient separation between humans and living apes, and thus also *Ramapithecus*' position in the human evolutionary tree. For example, comparisons of chromosome structure suggested that chimpanzees and gorillas are more similar to humans than to orangutans (Klinger *et al*. 1963). An even more substantial challenge to fossil-based views on the human–ape relatedness came from the rapidly developing field of molecular biology. Interspecific comparisons of the structures of various molecules, such as the amino acid sequences of the haemoglobin molecule, found that human, chimpanzee and gorilla were almost identical in appearance in this regard (Zuckerkandl *et al*. 1960). As the 1960s progressed, further molecular similarities between humans and apes, especially the African apes, were documented (Goodman 1963, 1974, 1996, Sarich & Wilson 1966, 1967a, b, Wilson & Sarich 1969). Molecular biologists suggested that amino acid mutations in molecules happened with predictable regularity over evolutionary time. Thus, the number of amino acid substitutions between the DNA of different species could be used to calculate the divergence dates of their respective lineages from each other. In the case of humans and living great apes, this 'molecular clock' suggested divergence dates that were much more recent than the dates arrived at by palaeoanthropologists who studied fossils. For example, based on studies of the albumin molecule, Sarich and Wilson (1967a) suggested that humans and the African great apes shared an ancestor as recently as 5 million years ago, in the Pliocene. As Goodman (1963: 400) stated, "man is the closest relative of the African apes, after which the orang-utan and then the gibbon are the next closest relatives". He added provocatively that "the serological affinities could be represented by placing all the recent hominoids in the single family Hominidae with *Gorilla*, *Homo* and *Pan* grouped together in the subfamily Homininae" (*ibid*.: 403).

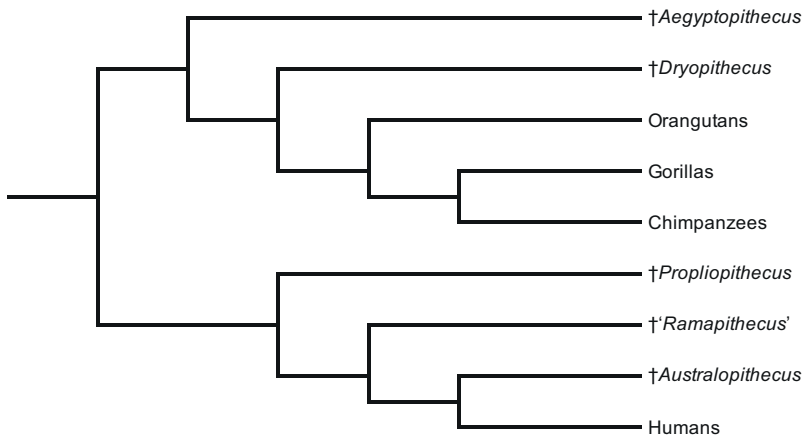

Fig. 3. Phylogenetic relationships of selected living and fossil taxa of primates, according to Kurtén (1972); † = extinct taxa. Note that *Ramapithecus* is no longer considered a valid taxon.

Kurtén and the 'not from the apes' hypothesis

For Kurtén, the late 1960s and early 1970s were a time of prolific literary output, and in addition to research papers, he published several books (Werdelin 1992). Some of these, such as *The Age of Mammals* (Kurtén 1971a) and *The Ice Age* (Kurtén 1972b), were not specifically about human evolution, but in both Kurtén discussed at some length the Fayum primates and their significance for human evolution. Kurtén, like Simons, considered *Propliopithecus* a likely human ancestor. Specifically, Kurtén thought that in addition to the small canine teeth, the shape of *Propliopithecus*' premolars as well as the shape of its tooth row were especially human-like; the latter was parabolic as in humans, rather than U-shaped as in living great apes. *Aegyptopithecus*, however, had in Kurtén's view too ape-like a dentition, which made it more likely to be an ancestor of the living great apes instead (Kurtén 1971a, 1972b).

In the early 1970s, Kurtén also published a book wholly devoted to human evolution. The book, which was first published in Swedish in 1971 and the next year in English, was called *Not from the Apes*. The sensational title referred to Kurtén's thesis that human ancestors had never passed through an ape-like evolutionary stage and humans had thus strictly speaking not evolved from 'apes'. Curiously, however, both in this book and in his other publications, Kurtén was rather vague regarding the precise definition of 'ape'.

Kurtén, being an expert on dentitions, based his argument mainly on tooth and jaw shape. It is worth pointing out that Kurtén did not study the relevant Fayum primate and *Ramapithecus* fossils personally; he based his hypothesis on data in the literature. He considered teeth in particular to be 'key characters', i.e. characters that should be given special weight when reconstructing relationships between different taxa, and said that "the teeth give us all the necessary [key characters] as far as apes and men are concerned" (Kurtén 1972a: 47). If uniquely human dental characteristics could be traced back to *Propliopithecus*, the human lineage must therefore, according to Kurtén, have been distinct from the lineage leading to modern great apes since at least the Oligocene, or for ca. 35 million years (Fig. 3).

Ramapithecus was also of great importance to Kurtén's hypothesis. For many years, he had supported the view that *Ramapithecus* was not only a hominid in the traditional strict sense, but a direct human ancestor. In his first book devoted to human evolution, *Människans utveckling* (Kurtén 1963), he had still expressed himself cautiously by stating that *Ramapithecus* may have been the ancestor of later hominids, but may also have been an evolutionary dead end that became extinct without leaving descendants. However, only two years later, in a foreword to the Swedish translation of William Howell's book *Mankind in the Making*, Kurtén stated that "there are no reasonable grounds for doubt" ("*[d]et finns ingen rimlig grund att betvivla*" in

the original) that ramapithecines were human ancestors (Kurtén 1965: 10). By the time that he wrote *Not from the Apes*, Kurtén effectively considered it an established fact that *Ramapithecus* was a human ancestor, and he speculated on its preferred environment and habits, including social structure and tool use.

In *Not from the Apes*, Kurtén rejected the possibility of a close kinship between humans and African great apes by stating that "[t]here seems to be no physical possibility that man could be more closely related to the living African apes than to the orang" (Kurtén 1972a: 43–44). He was dismissive of the molecular evidence that suggested a close relationship between humans and especially African great apes. Kurtén wrote (*ibid*.: 44): "The serological and chromosomal evidence is not really historical; it just shows present resemblance and difference but not how, when or why they have arisen. That they reflect degrees of affinity in descent is simply a hypothesis, and it stands or falls on its compatibility with historical evidence. In the present case, the historical evidence shows that the hypothesis is untenable."

Despite its title, less than a third of *Not from the Apes* specifically dealt with the hypothesis of an ancient, separate evolutionary origins of the human lineage. The rest of Kurtén's book was about human evolution more generally, including discussions of the biology and behaviour of extinct hominids. Kurtén also speculated on the possible direction of future human evolution.

Although *Not from the Apes* became one of Kurtén's internationally best-known books, its reception by the scientific community was lukewarm, or even negative. While the book's reviewers mostly praised its originality of thought, few of them found Kurtén's hypothesis convincing. For example, Marten (1972: 530) wrote that "It is […] unfortunate that Kurten should have based his book on the poorly supported hypothesis that the ancestors of man and the apes separated more than 35 million years ago. This flaw greatly reduces the value of an otherwise enjoyable book […]. The reader is largely presented with opinions, not facts, and this cannot be justified merely as a means of avoiding complexity." Marten concluded his review by saying that "[l]et us hope that the readers of this book […] will realize that Kurten should not be taken seriously" (*ibid*.).

As for other reviewers, Washburn (1973) took issue with Kurtén's contention that humans are morphologically 'primitive', as well as with the casual dismissal of serological and chromosomal data. Wilkinson (1973: 534) compared Kurtén's writing style unfavourably with that of two other science popularisers, Robert Ardrey and Desmond Morris, stating that Kurtén's book "lacks even the entertainment value which partially saves the others". Lipson and Pilbeam (1976: 442), in turn, stated with reference to Kurtén's book that "any theory of pre-pongid divergence for the Hominidae […] does not represent a very economical hypothesis."

New data and new interpretations of the primate fossil record

Throughout most of the 1970s, the occasionally acrimonious debate between palaeoanthropologists and molecular biologists about the divergence date between human and ape lineages centred on the position of *Ramapithecus* in hominid phylogeny (e.g. Leakey 1970, Wolpoff 1982, Lewin 1989, Goodman 1996, Beard 2004). The small amount of available fossil material was a major limitation, and few researchers (including Kurtén) had had an opportunity to examine the *Ramapithecus* fossils personally. However, one year after the publication of the English edition of *Not from the Apes*, Walker and Andrews (1973) published a new reconstruction of the mandible shape of *Ramapithecus*. Their results suggested that its dental arcade had been reconstructed incorrectly. It was V-shaped instead of parabolic, and thus rather less human-like than had been thought (Walker & Andrews 1973, Greenfield 1978). Greenfield (1978) remarked upon the similarities between the dental arcades of *Ramapithecus* and *Sivapithecus*, another fossil ape from the Miocene of Asia, and suggested that the relationship between these taxa should be re-examined. New fossil discoveries of early hominids in East Africa further weakened the hypothesis that some Miocene primates already had human-like dentitions. Circa 3.7 million-year old *Australopithecus afarensis*, an undoubted early hominid, had a dental arcade that was almost U-shaped and

thus ape-like rather than human-like in appearance (*see* Johanson & Taieb 1976: fig. 4).

By the late 1970s, even the strongest supporters of *Ramapithecus*' status as a human ancestor were beginning to have doubts (e.g. Pilbeam 1979). New fossil discoveries made at this time finally showed beyond reasonable doubt that *Ramapithecus* was essentially the same animal as the earlier described *Sivapithecus*, and the names were thus synonyms, with *Sivapithecus* having priority (Greenfield 1979, 1980, Andrews & Cronin 1982, Kay 1982, Pilbeam 1982). New morphological studies of *Sivapithecus* fossils suggested that it, and thus also '*Ramapithecus*', was very similar to the orangutan, and apparently its close relative if not its ancestor (Andrews & Cronin 1982). Greenfield (1980) presented the original suggestion that *Sivapithecus* might have been the last common ancestor of both humans and the living great apes. He accepted the biochemical evidence that suggested a closer relationship between humans and African great apes than between the latter and the orangutan; thus, according to his hypothesis the *Sivapithecus*-like traits of the modern orangutan were primitive retentions that were later lost in the lineage leading to African great apes and humans. However, most subsequent researchers have considered *Sivapithecus* too orangutan-like to be a possible human ancestor (e.g. Cameron & Groves 2004, Andrews 2015, Urciuoli & Alba 2023). By the mid-1980s, most researchers had abandoned the hypothesis that *Sivapithecus* ('*Ramapithecus*') was part of the human lineage (Lewin 1989, Pilbeam 1996).

Similar re-evaluations took place regarding the Fayum primates. New fossil discoveries and comparative studies found no morphological support for the hypothesis of a separate human lineage extending back to the Oligocene (Kay *et al*. 1981, Simons 1995). For example, the relatively small canines of *Propliopithecus* were found to be more likely partly a result of heavy erosion that the fossils were subjected to, and partly due to sexual dimorphism, with the smaller-toothed individuals apparently being females (Fleagle *et al*. 1980, Kay *et al*. 1981). Today, most researchers consider *Propliopithecus* and *Aegyptopithecus* to be closely related, with both being basal catarrhine primates that are not direct ancestors of extant apes (Williams *et al*. 2010).

Thus, by the 1980s, Kurtén's views on human evolution had become increasingly untenable. In his later publications on this subject, he had to modify his hypothesis. *Not from the Apes* was reprinted in 1984, and while the main text remained unchanged, Kurtén had added a new preface. There he wrote that "Recent finds of late Miocene apes […] now placed in the genera […] *Sivapithecus*, and *Ramapithecus*, indicate that they are all related to the orang […] and definitely off the human line" (Kurtén 1984: x). However, Kurtén was still unwilling to accept fully the molecular evidence. While admitting that "the molecular changes give excellent information on the timing of branching points in evolution" (*ibid*.: xi), he nevertheless suggested, while referring to inconsistencies between the results of different molecular studies, that "it seems that the emergence of a uniquely human line of descent may have occurred, very approximately, ten million years ago" (*ibid*.: xii). Thus, even in the 1980s Kurtén was inclined towards favouring a relatively early separation of the human lineage from the lineage leading to the African great apes.

Also in his final book on human evolution, *Our Earliest Ancestors*, which was published in Swedish in 1986 and posthumously in English in 1993, Kurtén was equivocal on the topic of human–ape evolutionary separation. While conceding that the picture of the relationship between humans and great apes offered by molecular biology was "probably more exact" (Kurtén 1993: 8) than the one offered by morphology, he pointed out what were, in his view, problems with the molecular clock hypothesis. He also criticised phylogenetic systematics by pointing out that it "pays no regard to the organism's "life niche," to evolutionary breakthroughs and the acquiring of new lifestyles" (*ibid*.: 12). Finally, Kurtén wrote that, in the end, "whichever [classification] is preferred depends on one's personal philosophy" (*ibid*.: 12).

However, *Our Earliest Ancestors* may include a tacit admission by Kurtén that his original thesis was no longer defensible and perhaps even something of an embarrassment by this point. The book ends with a short bibliography where

he listed some of his own publications, such as *The Age of Mammals*. Interestingly, *Not from the Apes* was not included in the bibliography.

Kurtén and the 'aquatic ape' hypothesis

The 'not from the apes' hypothesis was not the only unorthodox idea concerning human evolution that Kurtén championed during his career. In *Our Earliest Ancestors*, he devoted several pages to discussing the so-called 'aquatic ape' hypothesis, originally developed by Hardy (1960) and later popularised by science writers such as Morris (1967) and Morgan (1982). According to Kurtén, the idea that human ancestors had gone through an amphibious stage "is based on a great deal of probability" (Kurtén 1993: 71). Specifically, he suggested that it could explain certain peculiar human traits such as hairlessness and bipedality.

Although it has enjoyed some popularity among non-specialists, the aquatic ape hypothesis has never been widely accepted by professional palaeoanthropologists (Langdon 1997, Foley & Mirazón Lahr 2014). One of the main arguments against it is the modern understanding of the timescale of hominid evolution. As noted, in the early 1960s it was widely believed that the human evolutionary lineage had been separate from that leading to the extant great apes for a very long time, supposedly leaving plenty of time for evolutionary experiments such as adaptation to an aquatic environment. Hardy (1960: 645) originally stated in his essay that "It is in the gap of some ten million years, or more, between *Proconsul* and *Australopithecus* that I suppose Man to have been cradled in the sea." However, the molecular revolution, which began in earnest later that same decade, dramatically shortened the evolutionary time available for a hypothetical aquatic phase in human evolution. If humans had shared a last common ancestor with chimpanzees as recently as ca. 5 million years ago, it effectively made the aquatic ape hypothesis incompatible with the known fossil record of early hominids.

That Kurtén was favourable towards the aquatic ape hypothesis as late as 1986 is interesting because it suggests that he still had not wholly abandoned the idea that humans have had a long evolutionary history separate from the great apes, and had not fully taken on board the implications of the results of the molecular studies. In *Our Earliest Ancestors* he suggested that the amphibious stage would have taken place "somewhere between seven to nine million years ago […] and a time approximately four million years later that marks the appearance of the first-known *Australopithecus*" (Kurtén 1993: 71). This statement was only barely compatible with the fossil evidence even at the time of Kurtén's writing in 1986, and since then, the late Miocene–Pliocene gap in the hominid fossil record has been further filled with discoveries of taxa such as *Sahelanthropus* (Brunet *et al*. 2002), *Orrorin* (Senut *et al*. 2001) and *Ardipithecus* (White *et al*. 1994, Haile-Selassie 2001).

As had been the case with *Not from the Apes*, Kurtén's colleagues were not greatly impressed by some of the ideas presented in *Our Earliest Ancestors*. Although Greiner's (1994) review was generally mostly positive, he criticized the amount of space devoted to discussing the 'aquatic ape' hypothesis. Similarly, Allen (1996: 272) singled out Kurtén's fondness for this hypothesis as a specific problem with the book, stating that "I cannot recommend *Our Earliest Ancestors* […] I found the coverage of material to be too superficial and selective (too much aquatic ape), even for a popular treatment".

Kurtén, the scientific individualist

"All zoologists agree that man is a primate, and there are few who do not admit *Homo* to the same large subdivision, suborder, as the apes. The only disagreement on this point comes from those who wish to derive man — or perhaps who wish that man had been derived — from a vaguely remote early Tertiary source independent of the origin of monkeys and apes." (Simpson 1945: 181).

These words by Simpson, which were a thinly veiled critique of letting personal beliefs influence the forming of scientific hypotheses, were directed towards scientists such as Osborn, and not at Kurtén, whom Simpson of course did not yet know at the time. Subsequently, Simpson is on record as having thought highly of Kurtén, who, in turn, returned the respect by unofficially

considering Simpson his intellectual mentor (Leikola 1992). Regarding the evolutionary relationship between humans and great apes, Simpson and Kurtén agreed on many issues, notably in their views on biological classification; both were willing to, or even preferred to, treat taxa as grades rather than clades. According to both men's views, humans and great apes should be classified in the separate families Hominidae and Pongidae, respectively, because they occupied separate "adaptive zones" (Simpson 1959, 1962, 1963, cf. Hagen 2009) or "life niches" (Kurtén 1993). Simpson, even more so than Kurtén, was also critical of the primate phylogenies arrived at by molecular biologists (e.g. Simpson 1964, cf. Dietrich 1998, Aronson 2002, Hagen 2009). Like Kurtén, he only reluctantly accepted the results of molecule-based phylogenetic studies, especially results that pertained to primate classification. For instance, while Simpson as early as 1963 was willing to accept that the African great apes might be more closely related to humans than orangutans were, he still insisted on classifying humans in a separate family, Hominidae, and placing all the living great apes and most of the then known fossil ones in Pongidae. Interestingly, in 1963 Simpson tentatively included *Ramapithecus* in Pongidae, not Hominidae.

Thus, Simpson considered humans to be something special and unique, worthy of separation into their own biological category, regardless of their phylogenetic affinity to the great apes. Many other contemporary evolutionary biologists also thought that human beings were somehow fundamentally different from other animals. For example, Julian Huxley thought that humans were the only extant animals capable of large-scale future evolutionary change (Huxley 1950). While Simpson disagreed with Huxley on this particular matter (Swetlitz 1995), Kurtén referred to Huxley's views with tentative approval in some of his books (1963, 1971a, 1972a). Exposure to such views on human uniqueness during his intellectually formative years may conceivably have influenced Kurtén's later views on human evolution.

On the other hand, it is also possible that Kurtén rejected, perhaps subconsciously, certain hypotheses for partly non-scientific reasons. In particular, it is interesting to speculate on his attitude towards Weinert's 'summoprimate' hypothesis, with which, as noted, it is reasonable to presume that Kurtén was at least superficially familiar. Kurtén's lack of enthusiasm for this hypothesis may have been due to its originator's association with Nazi Germany; Weinert, like several other German anthropologists, was a member of the National Socialist Party before and during the Second World War (Proctor 1988, Junker & Hoßfeld 2002, Weikart 2013). Regrettably, it is not possible to be certain on this matter, as Kurtén never wrote an autobiography where he would have revealed what had influenced his thinking and his attitudes during his lifetime.

Donner (2014: 5) described Kurtén as "basically an old-school individualist rather than a team player, and although internationally well-connected, definitely no organizer of collaborative consortia". This view is supported by an analysis of Kurtén's bibliography. His near-complete publication list includes 192 items (Werdelin 1992). Of these, only 21, or ca. 11%, were co-authored. In the ten-year period 1962–1971, when Kurtén had 56 publications (or ca. 29% of the total output during his career), he was the sole author of all of these. It was during this time that he did the research for and wrote *Not from the Apes*. Perhaps the book's main thesis would have been different and more conventional if Kurtén had not written it in relative intellectual isolation, without access to human fossil material, and without being exposed directly to alternate views by professional palaeoanthropologists. However, although Kurtén undoubtedly was influenced by the opinions of his colleagues, it is important to stress that he was also, to a considerable degree, an independent and original scientific thinker. It is a testament to his flexible intellect that he could appreciate the potential importance of unconventional, minority views in science.

Since the 1980s, it has become widely accepted among scientists that the phylogenetic relatedness between humans and chimpanzees, and indeed gorillas and even orangutans, is very close (Fig. 4). So close, in fact, that it is appropriate to include the living great apes in the same family as humans, i.e. Hominidae (Groves 2001, Bradley 2008, Cartmill 2018, Almécija *et al*. 2021). In other words, this means that humans have not just evolved from apes but *are* 'apes'

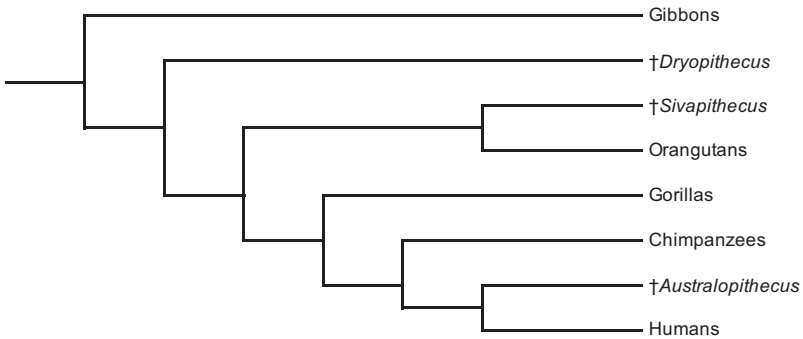

Fig. 4. A representative current phylogenetic tree of the relationships of selected fossil and living primate taxa, modified from Urciuoli and Alba (2023); † = extinct taxa. Note that the respective branching orders of gibbons, orangutans, gorillas and chimpanzees relative to humans are the same as in Weinert's (1932) tree (*ibid*. fig. 2). Note also that '*Ramapithecus*' is now included in *Sivapithecus*.

in a biological and phylogenetic sense. Most workers today agree that the last common ancestor of humans and chimpanzees lived between about four to eight million years ago (Hobolth *et al*. 2007, Besenbacher *et al*. 2019). However, there are also recent studies that have arrived at older divergence date estimates, some of them even pushing the divergence date back to earlier than ten million years ago, i.e. well into the Miocene (e.g. Langergraber *et al*. 2012, Moorjani *et al*. 2016). It has been suggested that the exact date for the divergence of human and chimpanzee lineages may be unknowable, because it is likely that hybridisation between human and chimpanzee ancestors has taken place since lineage divergence (Patterson *et al*. 2006, Bradley 2008). Thus, the final word regarding the timing of the human–chimpanzee lineage divergence has surely not yet been said. However, it seems unlikely that Kurtén's 'not from the apes' hypothesis will be vindicated by future research.

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