Human evolution and the origins of Stone Age clothing

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Zusammenfassung

Die Evolution des Menschen und die Ursprünge der Kleidung in der Steinzeit

Das ›Standardnarrativ‹ zur Entwicklung der menschlichen Kleidung sieht deren Entstehung in erster Linie im Zusammenhang mit der Anpassung an klimatische und ökologische Bedingungen, wonach sie im Wesentlichen der Thermoregulation des menschlichen Körpers dient. Mit der Zeit scheinen sich die funktionalen Aspekte der Kleidung jedoch zunehmend in Richtung sozial bedingter Gründe für das Bekleiden des Körpers zu verschieben. Der vorliegende Beitrag untersucht die wissenschaftlichen Belege für den evolutionären Verlust der menschlichen Körperbehaarung, kombiniert dabei Daten aus verschiedenen Disziplinen, darunter molekulargenetische Untersuchungen an Menschen und Läusen, überprüft die archäologischen Belege für die früheste Besiedlung der höheren Breitengrade und hinterfragt – durch die Diskussion der Zusammenhänge zwischen den verschiedenen disziplinären Ansätzen – die Gültigkeit des ›Standardnarrativs‹. Der vorliegende Beitrag diskutiert eine Reihe von Voraannahmen, die den meisten Interpretationen zugrunde liegen und die hauptsächlich durch die verzerrte, selektive Überlieferung vergänglicher Materialien in den älteren Steinzeiten geprägt werden. Er kommt zu dem Schluss, dass die Frage, wann Kleidung erstmals aufkommt, weitgehend unbeantwortet bleiben muss, weist jedoch darauf hin, dass Kleidung möglicherweise viel tiefer in der menschlichen Vergangenheit verwurzelt ist als allgemein angenommen, und schlägt vor, dass Textilien der Erfindung der Lederbekleidung vorausgingen.

Schlagwörter Thermoregulation, menschliche Ektoparasiten, Molekulargenetik, Kälteanpassung, Zerrbilder aufgrund von leicht vergänglichen Materialien

Summary

The ›standard narrative‹ of the evolution of human clothing sees its emergence primarily in the context of an adaptation to climatic and environmental constraints, basically serving issues of thermoregulation of the human body. With time, the functional aspects underlying clothing seem to shift towards socially induced reasons for clothing oneself. This contribution reviews the scientific evidence for the evolutionary loss of human body hair, combining data from different disciplines including human- and louse-genomic studies, reviews the archaeological evidence for the earliest occupation of the higher mid-latitudes, and – by discussing the interlinkages between the different approaches – questions the validity of the ›standard narrative‹. The present contribution addresses the massive biases underlying most interpretations, which are mainly hampered by the poor preservation of perishable materials in early Stone Age periods. It concludes that the question of when clothes were first invented remains largely unanswered but indicates that clothing may be much more deeply rooted in the human past than generally assumed, and proposes that textiles preceded the invention of leather clothing.

Keywords Thermoregulation, human ectoparasites, genomics, cold adaptation, preservation biases of perishable materials

From the »Naked Ape« …

Described as »naked apes« (Morris 1967), modern humans *(Homo sapiens sapiens)* are the representatives of the only species in the Primate order that is not fully covered in hair. Why and when modern human ancestors lost their fur and evolved near-naked skin is a matter of intensive scientific debate (e.g. Best et al. 2019), but most likely this process was triggered by multiple drivers.

The near complete absence of body hair that characterises human skin arrives together with major changes in the fabric and function of epidermal and deeper-layered tissues: An extremely high body surface cover of eccrine sweat glands and their high density are characteristics of human skin – unparalleled in other species in the Primate order (Best/Kamilar 2018) – and allow for enhanced thermoregulatory capacities of the human body (see discussion in Notely et al. 2024). It is argued that the related capaci-

ties for sweating were essential to perform »high physical activity in open, hot, semi-arid environments« (Best et al. 2019, 331; cf. Blumenthal et al. 2017) like the African savannahs, where food resources were widely dispersed. Roughly between 1.8 and 1.5 million years ago, these epidermal changes seem to have co-evolved with a near-modern human skeletal architecture and body stature (e.g. Wang/Crompton 2004; Haeusler et al. 2011; Holliday 2012), which – together with enhanced sweating capacities (Best et al. 2023) – would have enabled endurance running and therewith persistence hunting, an important strategy practiced amongst many contemporary hunter-gatherers to successfully drive prey into heat exhaustion (Bramble/Lieberman 2004; Liebenberg 2006).

In addition, genetic studies of the variation at the melanocortin 1 receptor (MC1R) locus (known to produce a protein that affects the pigmentation of skin and hair, studied in different human populations and compared with chimpanzee data) allow age-modelling of the timing when humans may have lost their body hair (Rogers et al. 2004). The genetic data analysed hint at the »adoptive evolution for sun-resistant MC1R alleles« in early human evolution (Rogers et al. 2004, 105). Based on their calculations, Rogers and colleagues suggest that ancestral humans »have been hairless savannah-dwellers for at least 1.2 million years« (Rogers et al. 2004, 107; cf. Fig. 1: centre, red typo). However, the mathematical models employed to explain today's genetic variability depend on the assumed size of an initial African population in which mutations appeared successively. But the authors also assert: »No matter how large we imagine the African population to have been, we will not conclude that the most recent selective sweep occurred less than 560 000 years ago« (Rogers et al. 2004, 107). With reference to the paucity of material evidence for clothing preserved from the Palaeolithic, they further state »that humans were naked before they were clothed« (Rogers et al. 2004, 107)[1].

… to the first dressed humans?

As mentioned above, the evolution of modern human hairlessness most likely had multiple drivers. Pagel and Bodmer (2003) argue that ectoparasite loads would have been reduced as a result of evolving human hairlessness. In consequence, the spread of related diseases would be limited, and survival enhanced. According to these authors, with the dedicated deployment of clothes, human-built dwellings, and the controlled use of fire, the lack of the protective properties of body hair could have been compensated for. Furthermore, it would have been easily possible to clean clothes and shelters »if infested with parasites« (Pagel/Bodmer 2003, S117) largely abandoning them. Clothes, dwelling structures and the habitual use of fire would have further paved the way for early human geographical expansion into climatically less favourable and mostly colder regions (cf. Gilligan 2010).

However, despite a few early indications for the use of fire (e.g. Alperson-Afil 2008), at present it seems that its controlled use did not become regular practice significantly before ~400 ka[2] (Roebroeks/Villa 2011; Roebroeks et al. 2021). Even the much younger, dense Upper Pleistocene archaeological record of Ice Age Europe still shows that fire was not in constant use (e.g. Dibble et al. 2017; Murphree/Aldeias 2022). Arguments for the earliest appearance of clothing are even less straightforward, as perishable materials rarely survive in the archaeological record (see review in d'Errico 2024; cf. Gilligan 2010, and a series of papers in this volume). Similarly, unambiguous evidence for shelter-like dwelling structures (cf. Barham et al. 2023) does not exist until quite recently (e.g. Nadel 2003), demanding critical evaluation of potential features and structures (Kolen 1999).

Nevertheless, even with the more regular use of the above (protective) technologies, humans never rid themselves fully of parasites (Boutellis et al. 2014). It is only since the (late) Middle Pleistocene/early Upper Pleistocene that new parasites appeared: the human clothing louse (Fig. 1: left, violet), which diverged from human head louse ancestors between roughly 691 000 and 29 000 years ago (at 95 % probability density), according to statistical modelling of available DNA data of recent lice (Toups et al. 2011). An age-estimate of 83 ka has been calculated for the highest posterior probability for this divergence, a median of 170 ka and a mean value of 229 ka (Toups et al. 2011). The lice DNA data further suggest »that the use of clothing likely originated with anatomically modern humans in Africa« (Toups et al. 2011, 29). This is argued to be in line with other developments toward the evolution of human »behavioural modernity« around the Middle to Upper Pleistocene transition, »including the increasing use of ochre for various protective and symbolic purposes and the production of personal ornaments«, suggesting »that these practices were well established [in Africa] by at least 160 000 to 140 000 years ago« (d'Errico 2024).

A need for clothing in the Ice Age cold?

The genetic data indicate that ancestral humans most likely lost their body hair either in the late Early Pleistocene or, at the latest, in the early Middle Pleistocene (Rogers et al. 2004), i.e. around the Mid-Pleistocene Transition (MPT), a period between ~1.25 million years and 750 ka ago (Fig. 1) during which the global climate system slowly changed from the roughly 40-kyr[3] cyclicality of glacial-interglacial cycles to the present period – characterised by 100-kyr cyclicality – with more pronounced differences between longer glacial (even numbered Marine Isotope Stages [MIS]) and shorter interglacial (odd MIS numbers) climate conditions (e.g. Herbert 2023).

At the present state of knowledge, early humans had already expanded northwards, beyond the limits of the

1 A much earlier date for the loss of body hair (~3.3 million years ago) has been proposed based on the origin of pubic lice in humans (Reed et al. 2007; cf. Gilligan 2010).

2 ka = kilo annum (i.e. 1000 years).

3 kyr = kilo year (i.e. 1000 years), here used exclusively for the astronomical age-scale.

African continent, by more than ~2.1 million years ago, quickly reaching eastern Asia (Zhu et al. 2018), and moving into the southern half of Europe (here, defined as south of ca. 47.5°N) probably as early as 1.7–1.3 million years ago (e.g. Arzarello et al. 2007; Berto et al. 2024; López-García et al. 2015)[4], but at the latest by ~1.4–1.2 million years ago[5]. According to population modelling, the northern half of Europe north of the Alps may have been occupied soon thereafter – between 1.16 million years and 913 ka ago (Key/Ashton 2023; cf. Despriée et al. 2024). The first archaeological evidence north of 47.5°N, i.e. in the northern mid-latitudes (Fig. 1: centre section), dates to ~950 ka (MIS 25) or ~850 ka (MIS 21), with Happisburgh 3 in eastern England being the only securely dated late Early Pleistocene site in primary context located this far north (Parfitt et al. 2010; Ashton et al. 2014)[6]. Potentially further evidence for an early ancestral human settlement this far north, dating around 800 ka (MIS 19) or ~700 ka (MIS 17), comes from a few localities nearby (Parfitt et al. 2005; Key/Ashton 2023).

Whereas the above northern European evidence for early human occupation is exclusively linked to interglacial contexts, the site of Moulin Quignon in northern France, which produced amongst the earliest Acheulean tools in Europe, has been dated to between 670 ka and 650 ka and falls in the beginning of MIS 16, representing the first northern European archaeological site that provides evidence for human presence under cold climatic conditions (Antoine et al. 2019). It was probably the ability to cope with such cold conditions that was required for a more persistent human presence in the north that can neither be traced before MIS 15–13 in Europe (Jöris 2014; cf. Key/Ashton 2023), nor in northern Asia.

The Early and Middle Pleistocene dispersals of ›super-archaic‹ and ›archaic‹ humans across Eurasia further led to their (genetic) divergence from ancestral human populations (Fig. 1: centre; cf. Bergström et al. 2021). Genetic differences between the Middle Pleistocene archaic humans and modern humans make it possible to distinguish the Neanderthals, which were spread across western Eurasia, from the so-called Denisovans in the east (see Zeberg et al. 2024). Most importantly, given the overall genetic similarities between the three groups, Zeberg et al. emphasise »that the genetic basis of what constitutes a modern human is best thought of as a combination of genetic features, where perhaps none of them is present in each and every present-day individual«, resulting from repeated and considerable admixture between these populations (e.g. Zeberg et al. 2024; Bergström et al. 2021).

Calculated through statistical analysis of nuclear DNA variability, the major split between archaic and modern human populations has been estimated to have taken place between ~765 ka and 550 ka (Meyer et al. 2016; Prüfer et al. 2014) or between ~630 ka and 520 ka (Prüfer et al. 2017)[7], with Neanderthals and Denisovans diverging from each other more than 430 000 years ago (Meyer et al. 2016; cf. Prüfer et al. 2014).

A more recent study of mitochondrial DNA variation, however, highlights that the age estimate for the most recent common ancestor of both modern humans and Neanderthals, who is supposed to pre-date the population divergence, may have lived closer to 400 ka (Levinstein Hallak/Rosset 2024; cf. Endicott et al. 2010; Rieux et al. 2014)[8]. In contrast to this late date, Levinstein Hallak and Rosset (2024) further calculate an age of ~841 ka for the most recent common ancestor of modern humans and Denisovans.

Cold adaptation vs. protective clothing?

In conclusion, the combined data compiled seem to confirm the idea that archaic humans did indeed expand across Eurasia well after having lost their hair (Rogers et al. 2004), during a time of increasing climatic harshness in northern latitudes (see above). With regard to the question of whether archaic humans required clothing to survive in the higher mid-latitude regions of Eurasia, it should be discussed to what degree they managed to cope with cold climate environments (Gilligan 2010). Although Neanderthals appear to have clearly preferred warmer habitats (e.g. Serangeli/Bolus 2008; Jöris et al. 2022), many aspects of Neanderthal physical anatomy (e.g. Buck et al. 2018; see discussion in Rae et al. 2011) and physiology (e.g. Steegmann et al. 2002) have been interpreted in favour of having been »hyper-adapted to living in cold environments« (Ocobock et al. 2021, and discussion thereof cf. Churchill 2006). However, our still limited understanding of the relationships between physical features (skeletal and body morphology), physiological processes (metabolism and energetic flows from diet to digestion), and the behavioural underpinnings of human lifeways, call for caution in the interpretation of cold-

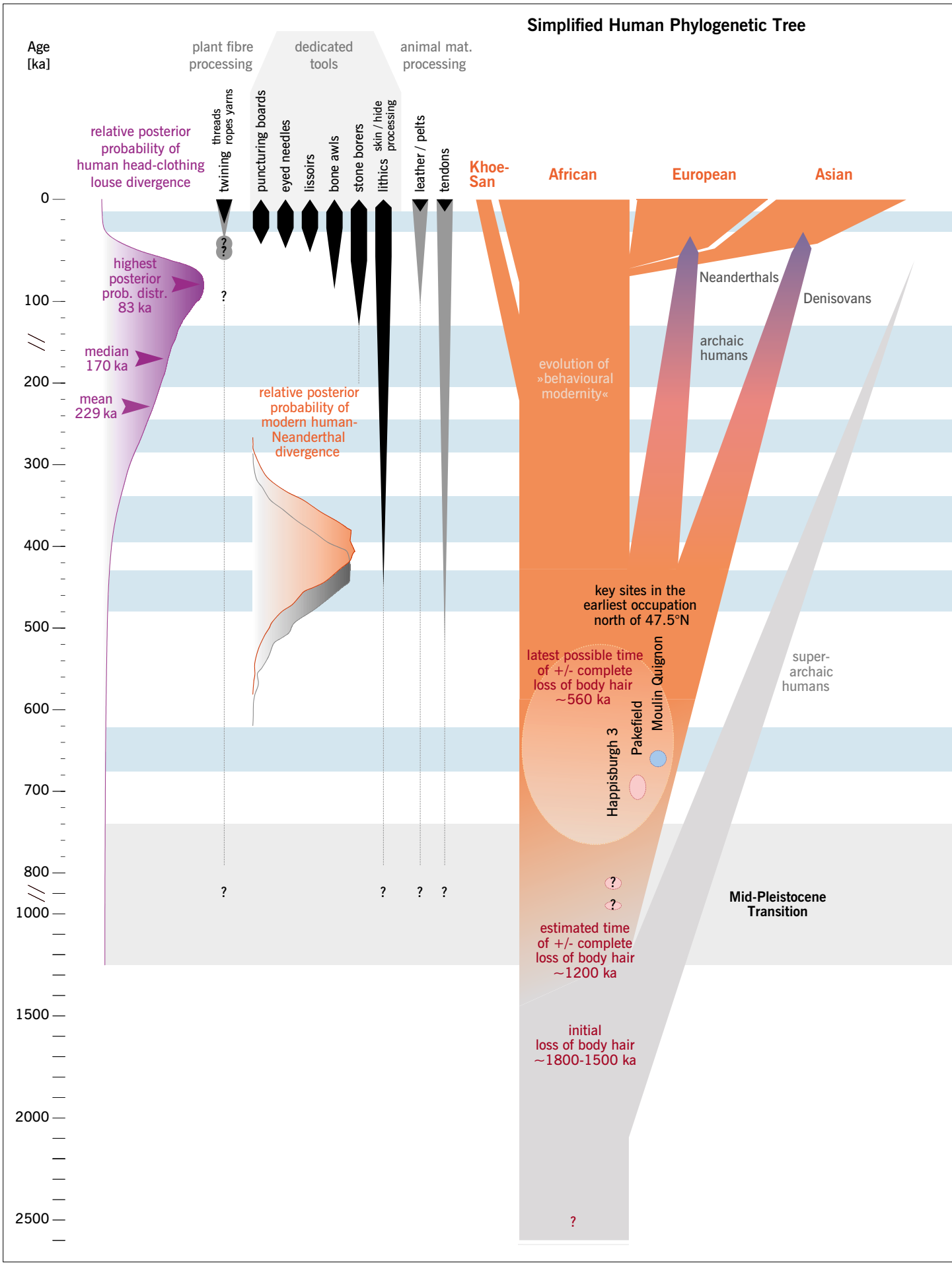
4 For a younger age estimate of the Pirro Nord lithic and faunal assemblages, see Duval et al. 2024, assigning the assemblages a maximal age of ~800 ka.

5 E.g. Huguet et al. 2017; Huguet et al. 2025; Blain et al. 2016; Lozano-Fernández et al. 2015; Despriée et al. 2024. Claims for an early human presence at the west Ukrainian site of Korolevo near ca. 48°N some ~1.4 million years ago (Garba et al. 2024) must be regarded critically (Demidenko 2024).

6 Note that some scepticism concerning the age of the site remains, claiming an age of < 600 ka (Westaway 2011).

7 These estimates are roughly in line with earlier metagenomic studies that concluded that Neanderthals and modern humans »share a most recent common ancestor ~706 000 years ago, and that the human and Neanderthal ancestral populations split ~370 000 years ago, before the emergence of anatomically modern humans« (Noonan et al. 2006, 1113). Similar calculations have been deduced in a study of Neanderthal Y-chromosome DNA, indicating that the most recent common ancestor between Neanderthals and modern humans lived around 588 ka (95 % confidence interval, ranges between 806 ka and 447 ka; Mendez et al. 2016).

8 Detailed studies of early human dental morphology point towards a much older age estimate for the last common ancestor of Neanderthals and modern humans (Gómez-Robles 2019). Áida Gómez-Robles argues that dental evolution would have been unexpectedly rapid, if one assumes a divergence of Neanderthals and modern humans later than ~800 ka ago. Respecting an average speed for changes in dental morphology, the best age estimate would place the last common ancestor of Neanderthals and modern humans between ~850 ka and 1.2 million years ago. In good agreement with these age estimates are the results of geometric-morphometric studies aimed at understanding the phylogenetic position of the c. one-million-year-old Yunxuan cranium, China, that hint at ages between ~1.0 and ~1.4 million years ago for the respective divergences of Neanderthals and Denisovans from modern humans (Feng et al. 2024).


Simplified Human Phylogenetic Tree
Age [ka]
plant fibre processing
dedicated tools
animal mat. processing
threads
ropes
yarns
twining
puncturing boards
eyed needles
lissoirs
bone awls
stone borers
skin / hide processing
lithics
leather / pelts
tendons
relative posterior probability of human head-clothing louse divergence
highest posterior prob. distr. 83 ka
median 170 ka
mean 229 ka
relative posterior probability of modern human-Neanderthal divergence
Khoe-San
African
European
Asian
Neanderthals
Denisovans
archaic humans
evolution of »behavioural modernity«
key sites in the earliest occupation north of 47.5°N
latest possible time of +/- complete loss of body hair ~560 ka
Moulin Quignon
Pakefield
Happisburgh 3
super-archaic humans
Mid-Pleistocene Transition
estimated time of +/- complete loss of body hair ~1200 ka
initial loss of body hair ~1800-1500 ka
0
100
200
300
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700
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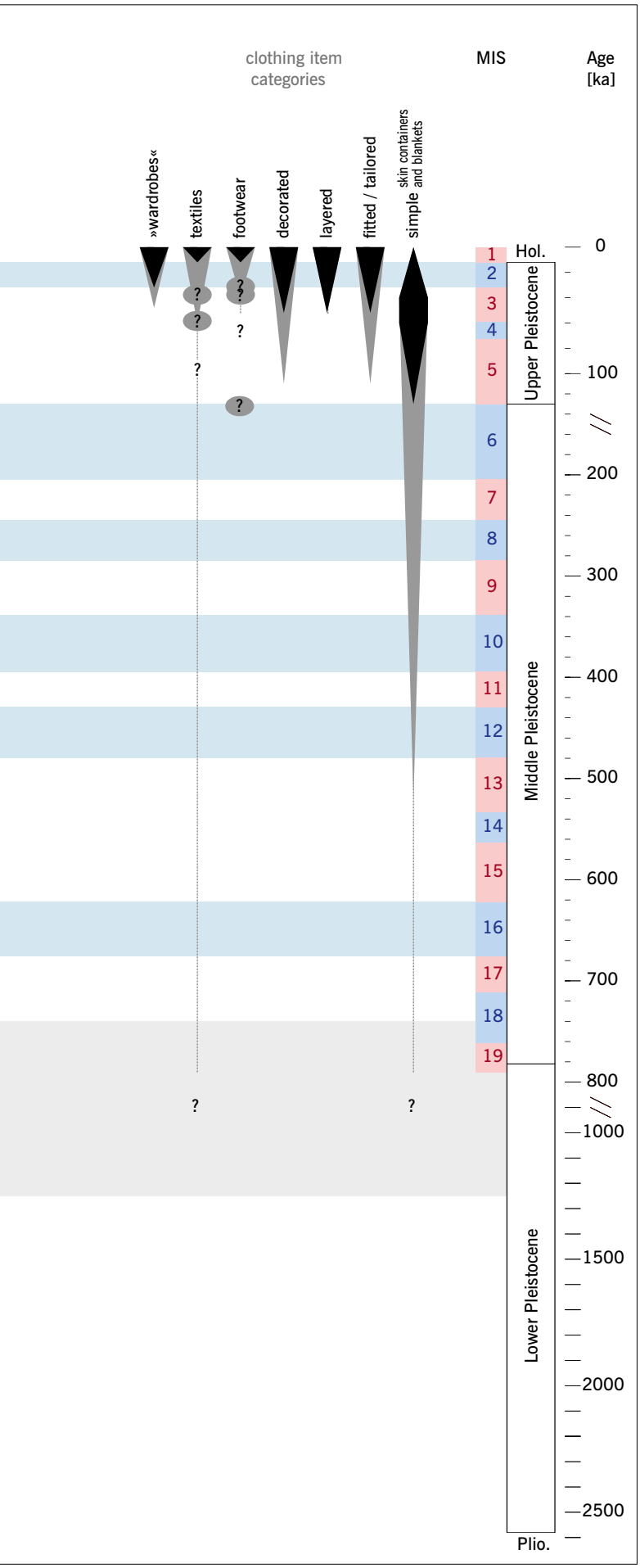
1000
1500
2000
2500



adapted features (Pomeroy 2023), as the chain of reasoning may easily become circular in that it follows the (logical) line of arguments emphasising that life in the north would demand cold adaptation, which should be expressed in biological as well as in cultural features.

Based on ethnographic data from recent modern hunter-gatherers, Nathan Wales (2012) has argued in this direction, emphasising that the surface of the body covered by clothes increases, the lower the mean temperatures of the coldest month become. For the colder intervals of the last glacial cycle, the study predicts that some Neanderthal pop-

Fig. 1 Simplified model of human phylogeny, based on combined genetic studies (centre; modified from Pimenoff et al. 2017), illustrating the divergence of super-archaic and archaic humans – the latter represented by Neanderthal and Denisovan populations – from (recent) modern humans (the oval ranging from 765 ka to 520 ka marks the split between modern human and archaic human populations according to nuclear DNA studies of Meyer et al. [2016] and Prüfer et al. [2014; 2017]), compared with posterior probability age estimates for the divergence of modern humans and Neanderthals (after Endicott et al. 2010, with two age estimates based on different models of the human-Chimpanzee divergence, sometimes assumed to date 6–7 million years ago [orange graph], another time assumed to date 6.5–7.5 million years ago [grey graph]) and for the divergence between human head and clothing lice (left, violet: modified from Toups et al. 2011). The genetic data are compared with well-proven (black) and potential (grey) evidence for different tools and technologies involved in the production of clothes shown as vertical time bars to the left of the phylogenetic tree, and with clothing items or categories shown to its right (in analogy to and modified from d'Errico 2024 and Gilligan et al. 2024 and various further sources, for details see text). Data are plotted against a vertical timeline of the Pleistocene (furthest right), bracketed between the late Pliocene (Plio.) and the Holocene (Hol.). The Mid-Pleistocene Transition between ~1.25 million years and 750 ka ago (Herbert 2023) is highlighted, as well as the record of Middle Pleistocene climate change (Lisiecki/Raymo 2005) of glacial (even numbered Marine Isotope Stages [MIS], shown in blue) and interglacial periods (odd numbered MIS, shown in red). The most severe glacial periods are highlighted as blue horizontal bars. Note that the age axis (vertical) changes twice at around 150 and 900 ka. Further explanations are given in the text.

Abb. 1 *Vereinfachtes Modell der menschlichen Stammesgeschichte, basierend auf kombinierten genetischen Studien (Mitte; modifiziert nach Pimenoff et al. 2017), das die Abspaltung ›super-archaischer‹ und ›archaischer‹ Menschen – letztere vertreten durch Neandertaler und Denisova-Menschen – von der Linie, die letztlich zu uns modernen Menschen führte, veranschaulicht (das Oval von vor 765 ka bis zu 520 ka markiert die Trennung von modernen und archaischen Menschen gemäß Kern-DNA-Untersuchungen von Meyer et al. [2016] und Prüfer et al. [2014; 2017]), verglichen mit Modellierungen des Zeitpunktes, nach dem die Divergenz von modernen Menschen und Neandertalern erfolgt sein dürfte (nach Endicott et al. 2010, mit zwei Altersschätzungen, die auf unterschiedlichen Modellen der genetischen Trennung von Chimpansen und modernen Menschen basieren, für die einmal ein Alter von 6–7 Millionen Jahren angenommen wird [orangefarbener Graph], ein anderes Mal ein Alter von 6,5–7,5 Millionen Jahre [grauer Graph]), und für die Trennung zwischen menschlichen Kopf- und Kleiderläusen (links, violett: modifiziert nach Toups et al. 2011). Die genetischen Daten werden mit gesicherten (schwarz) und potenziellen (grau) Belegen für verschiedene Werkzeuge und Technologien zur Herstellung von Kleidung verglichen, die als vertikale Zeitbalken links vom Stammbaum dargestellt sind, sowie mit Kleidungsstücken oder -kategorien, die rechts davon dargestellt sind (in Anlehnung an und modifiziert von d'Errico 2004 und Gilligan et al. 2024 sowie verschiedenen weiteren Quellen; Details siehe Text). Die Daten sind auf einer vertikalen Zeitachse des Pleistozäns (ganz rechts) dargestellt, das zwischen dem späten Pliozän (Plio.) und dem Holozän (Hol.) liegt. Der klimatische Wechsel am Übergang vom Frühen zum Mittleren Pleistozän zwischen ~1,25 Millionen Jahren und 750 ka vor heute (Mid-Pleistocene Transition: Herbert 2023) ist hervorgehoben, ebenso wie der wechselhafte Gang des Klimas im Mittleren Pleistozän (Lisiecki/Raymo 2005) mit Glazialen (gerade nummerierte Marine Isotope Stages [MIS], blau dargestellt) und Interglazialen (ungerade nummerierte MIS, rot dargestellt). Die strengsten Glazialperioden sind als blaue horizontale Balken hervorgehoben. Zu beachten ist, dass sich die Altersachse (vertikal) zweimal um 150 ka und 900 ka ändert. Weitere Erläuterungen finden sich im Text.*

ulations »would have covered up to 80 % of their bodies during the winter« months, likely including covering their hands and feet (Wales 2012, 781). Even though one is willing to follow the logic behind this argument, it is important to remember that empirical data in support of this hypothesis are scarce or even completely lacking. On the contrary, numerous foot imprints have been preserved at different Pleistocene sites throughout Eurasia (cf. Pastoors/Lenssen-Erz 2021 for an overview). Whenever their morphology is preserved at a high level of detail, which depends on the conditions during which the imprint formed (sediment grain size distribution, moisture content, etc.) and its taphonomic alterations thereafter (cf. Ledoux et al. 2021a), it is clear that the imprints generally represent individuals walking barefoot, lacking any type of footwear. The oldest hominin foot imprints preserved in Europe have been documented at Happisburgh in England (Ashton et al. 2014; Ashton 2021) – only 140 m distant from the locality that lays claim to the earliest occupation of northern Europe (see above): all bare feet. For pre-modern humans, only in a single case – Theopetra Cave in Greece, dating some ~130 000 years ago (Kyparissi-Apostolika/Manolis 2021) – were arguments put forward in favour of Neanderthal use of footwear.

Assuming that the foot imprint record does not stem exclusively from warm-climate warm seasons, one tends to argue against Wales' (2012) prediction. To the contrary, based on the footprint evidence, one would have to claim that the invention of footwear as thermal protection should have been a late invention. This is supported by noticeable differences in anatomical features of archaic and modern human phalanges, indicating that »supportive footwear was rare in the Middle Paleolithic, but that it became frequent« by the Upper Palaeolithic (Trinkaus 2005, 1515; Trinkaus/Shang 2008; cf. Trinkaus et al. 2021[9]). This claim is largely in line with some of the footprint evidence, hinting at the use of footwear during the mid-Upper Palaeolithic, well-studied in the cave of Cussac in France (Ledoux et al. 2021b; cf. Ledoux et al. 2021a).

The potential differences in footwear use between archaic and modern humans are mirrored in claims for differences in clothing (Collard et al. 2016) and closely follow the idea that archaic humans were equipped with simple, »probably [...] non-tailored clothing« (Wales 2012), whereas the ›standard narrative‹ says that mid-Upper Pleistocene modern humans wore more elaborate and sophisticated, fitted, tailored, probably layered and – most likely – decorated dresses (e.g. d'Errico 2024; Gilligan et al. 2024; Trinkaus/Buzhilova 2018). This feeds into the general view that ›proper‹ clothing was invented comparably late (cf. Toups et al. 2011 and discussion above) and that archaic humans were not so well adapted to meet the challenges that life in cold environments confronted them with (Gilligan 2007). However, the evidence for fitted, tailored, layered, and decorated clothing cannot be read only in terms of thermal insulation, as many aspects of sociality are interconnected with the types, ways, and many reasons why humans dress (e.g. Gilligan in this volume; d'Errico 2024).

Even though clothing fulfils multiple (social) purposes, it – of course – preserves functional aspects, as was central in Wales' (2012) study. In this context it is important to mention that recent modern humans display metabolic and insulative properties indicative of a »whole body cold adaptation« (Daanen/Van Marken Lichtenbelt 2016; cf. Hill 2023), allowing regulation of the body's heat balance through a range of processes that relate to specific physical and physiological properties of the human body (Daanen/Van Marken Lichtenbelt 2016; Pomeroy 2023). Brown adipose subcutaneous tissue and skin pigmentation play among the major roles in metabolic and insulative cold adaptation and are argued to have dispersed »out-of-Africa« with the dispersal of modern humans (Daanen/Van Marken Lichtenbelt 2016; cf. Ocobock et al. 2021). Following this argument, one may hypothesise that modern humans may be better adapted to a cold climate than archaic humans were. A recent study in three cultures in different regions of the globe in which individuals live (almost completely) naked addressed the metabolic feasibility to cope with cold-season temperatures around ±5° C (Hill 2023). Although their lifestyles are calorically costly, the study shows that basic metabolic rates and metabolic endurances allowed for levels of thermoregulation feasible to overcome periods »significantly longer than 50–180 days per year« (Hill 2003, 182), bridging the cold seasons in the different regions. These data, indeed, indicate that modern humans are well-adapted to get along with cold climatic conditions, and also explain our species' global distribution.

The extent to which archaic humans were equally adapted to sustain such costly metabolisms has been repeatedly discussed (Ocobock et al. 2021). In this context, not only regional climatic conditions need to be considered, but also body mass (Heyes/MacDonald 2015) and skin surface area (Churchill 2006), hinting at elevated basal metabolic rates in Neanderthals compared to modern humans. This would demand significant increases in caloric intake. Although attempted by Wales (2012), the data available at present are still too fragmented to allow for precise estimates of the bioenergetic demands of archaic humans in different climatic and seasonal context, and – as mentioned above – their presence in higher-mid latitudes seems to be restricted to milder or warmer periods (Jöris et al. 2022), rather than severe cold intervals. But genomic studies indicate that Denisovans contributed genetically to the high-altitude adaptation of modern Tibetans as well as to Inuit »adaptation to low temperatures, probably inducing brown fat« (Zeberg et al. 2024, 1052). Although these data provide some strong arguments for archaic humans' cold adaptation, it remains largely unanswered whether or not, and to which degree, they were able to cope with cold cli-

9 For examples of well-preserved younger Stone Age footwear, see Pinhasi et al. 2010 for a Chalcolithic leather-made shoe stuffed with loose grass, found in Armenia (cf. Hafner in this volume); for examples of early plant-fibre-made sandals, see contributions by Maria Herrero-Otal et al. and by Mario Mineo et al. in this volume. For claims of even older fibre-based footwear technologies, see Ollivier et al. 2017.

mate – especially during the cold season of the year – and whether or not they managed to deal with such conditions better than modern humans.

Deep, unknown roots of clothing?

It is generally assumed that the more elaborate clothes are, the more sophisticated the tools and technologies required for their production will be. This assumption opens the narrative arc in which the evolution of clothing is interpreted as having been ›simple‹ and ›primitive‹ in earlier times, and ›complex‹ and ›fancy‹ in later periods. Both the immense diversity of present-day human clothing and the archaeological record seem to give ample proof of the technical diversification and growing complexity of clothing manufacture over time. Starting with simple stone artefacts interpreted as borers that may have been used in the production of clothes, bone awls and lissoirs used for the perforation and smoothing of animal materials, eyed needles, and ›puncturing boards‹ are most generally interpreted in the context of the manufacture of clothes (d'Errico 2024; Gilligan et al. 2024). But often, the functional interpretation of some of these tool types is merely inferred solely from tool morphology, or is based on use-wear analyses, which are rarely backed by systematic large-scale and comprehensive experimental approaches (as a recent example for analytical progress in this field, see Ma et al. 2023). However, the most straightforward functional interpretation of a tool closely linked to clothing manufacture (but not exclusively reserved for such purposes!) is the eyed needle (d'Errico et al. 2018; Gilligan et al. 2024), even though recent finds hint at the existence of alternative methods for performing sewing tasks well without these enigmatic tools (Doyon et al. 2023). Personal ornaments are also often interpreted as applications sewn onto clothes (cf. d'Errico 2024; Gilligan et al. 2024); of these, the burial contexts at Sunghir in Russia provide the most impressive evidence, highlighting the social relevance of decorated garments (Trinkaus/Buzhilova 2018) that, in some cases, seem to closely resemble the traditional costumes most widespread in rural regions today. The above – to the greatest degree, indirect – evidence speaks of tailored and decorated clothing not before c. 40–50 ka, but hints at possibly much deeper roots when the first personal ornaments are considered as clothing applications, roughly around 100 000 years ago (e.g. Bar-Yosef Mayer 2020), i.e. at around the time when the clothing louse diverged from its head lice ancestors (Toups et al. 2011).

During the last few years, tools that are most generally associated with the production of clothing have been reported more and more frequently from late Middle Palaeolithic contexts (e.g. Soressi et al. 2013; Tartar et al. 2022; cf. Hallett et al. 2021). The same accounts for the use of bird claws and potentially of feathers as personal ornaments[10], which could be applied to clothes as decoration, and which may date back to as early as ~400 ka (Blasco et al. 2019). The evidence of Neanderthal footwear at around 130 ka, already mentioned above (Kyparissi-Apostolika/Manolis 2021), must be listed in this context, as well. Much older, however, is the use-wear evidence of hide processing or evidence for the extraction of tendons, dating back to ~450 ka to 500 ka or slightly older[11], potentially even with much deeper roots (cf. Carbonell et al. 1999).

When compared with the modern human record of clothing, all these data make it highly likely that Neanderthals used tools and materials for clothing production similar to those used and implemented by modern humans. The Neanderthals' tools for clothing manufacture were probably not as standardised as modern human tools were. Nevertheless, the chief reasons why we tend to think they were much simpler and less sophisticated are two-fold: (1) the lack of eyed needles, and (2) the absence of decorated burials, which are both usually interpreted as indicative of simple, not properly fitted, non-tailored clothing, lacking decorative applications (see discussion in Gilligan in this volume; d'Errico 2024; Gilligan et al. 2024). However, this logical, but also simplistic and reductionist view is, to an extreme level, biased by the lack of preservation of perishable materials the farther we look back into the past. In this context, it should be mentioned that the ›standard narrative‹ of the evolution of clothing places the origin of clothes made of animal materials chronologically before the emergence of clothing items made from plant fibres. But plant fibres are rarely preserved in earlier Palaeolithic contexts (e.g. Rots et al. 2015), and our still poor understanding of past plant processing and fibre technologies (see Rots/Tomasso in this volume[12]) hampers a systematic assessment of potentially older fibre-based clothing technologies, including the production of textiles and basketry, as is argued for the mid-Upper Palaeolithic (e.g. Soffer et al. 1998; Soffer et al. 2000; but cf. Valoch 2007 for a critical review), likely involving weaving (Soffer 2004), which is argued to have implications for the sexual division of labour (Soffer/Adovasio 2010; Soffer/Adovasio 2014). As contrasting evidence, only a single pre-Upper Palaeolithic example of twined fibres, interpreted as a cord fragment, has been reported to have been preserved, carbonised on a surface of a lithic artefact from the late Middle Palaeolithic site of Maras in France, dated to 41 000–52 000 years ago (cf. Hardy et al. 2020[13]). One can easily imagine how much our view of the Middle Palaeolithic would change if preservation conditions permitted similar discoveries in earlier periods.

10 Finlayson et al. 2012a; Finlayson et al. 2012b; Fiore et al. 2016; Radovčić et al. 2015; Romandini et al. 2014.

11 E.g. Keeley 1993; Parfitt 1999; Claud et al. 2019; Lemorini et al. 2020; Nicoud et al. 2022.

12 Cf. Conard/Rots 2024 and discussion in Kvavadze et al. 2009; Kvavadze et al. 2010; Bergfjord et al. 2010; cf. Nadel et al. 1994.

13 Criticism of this interpretation presented by Verle Rots and Sonja Tomasso in this volume, is based on questioning the context of the reported processed fibres. The carbonisation of the cord fragment and of other fibre materials in the specific layer is a major argument for their not being intrusive (Hardy et al. 2020).

Plant fibres at first?

With a more abstract view of the evolution of clothing, it is noteworthy that plant fibres are generally easier to access than faunal materials, lighter to transport, and that their processing requires simpler techniques, which are easier to learn. It is for these reasons that the use of plant materials – e.g. for dwelling and nest building – is also documented in many animal species. Even though many species have evolved protective behaviours for different types of dwelling and shelter, with Chimpanzees and Orangutans, for example, using leaves as ›rain hats‹ to protect against rain or intense sunshine or simply for comfort (e.g. Ingmanson 1996; Wich et al. 2009; Shumaker et al. 2011), clothing is seen as a technology or culture that is only found in humans. As such, the use of clothes is often classified as one of the hallmark behaviours distinguishing humans from animals. Such binary perspectives are deeply rooted in Western scientific reductionist approaches. The distinction of modern and archaic humans is only one of such reductionist concepts. Viewed in an evolutionary timeline, it is not surprising that wearing clothes or not frequently connotes attributes such as ›civilised‹ on the one hand and ›primitive‹ on the other – a dichotomous perspective that places the ›human culture of clothing‹ in opposition to an ›animal's biological nature‹ (see e.g. Brock 2007). ›Proper‹ and elaborate clothing would be expected to have emerged during the evolution of what is frequently called »behavioural modernity« (d'Errico 2024), which rather »originated with anatomically modern humans in Africa« (Toups et al. 2011, 29) than outside this continent in Eurasia, even though the »origins of modern human ancestry« – at present – cannot be securely tied to the African continent (Bergström et al. 2021).

Even if one interprets the divergence of the clothing louse from human head lice as the ultimate evidence for the regular, habitual covering of larger parts of the skin with garments, one should bear in mind that the divergence of the different species begins around the mid-Middle Pleistocene (Toups et al. 2011; Fig. 1: left, violet), indicative of early origins for clothing, and in line with Gilligan (2010) and other authors. But what did these early clothes look like? Given the poor preservation of old perishable material, discussed above, one can only speculate. Nevertheless, if one follows the arguments outlined here, that plant-fibre worked products would have been more easily available, producible, and transportable, one would assume that the origins of clothing are to be found in early textile-working. The 77 000-year-old evidence for potential fibre mats uncovered in South Africa at the site of Sibudu (Goldberg et al. 2009) hints at the production of larger textiles, which did not necessarily serve as clothes in a strict sense of dress, but were used in bedding or shelter. This possibility shows that we must widen our view from the narrow definition of clothing to any production of shelter made of organic materials, be it plant or animal based: the technologies required would be entirely the same, whether they were used as a ›second skin‹ worn directly on the skin, or implemented at a distance to control the micro-climate within a spatially-limited shelter. Mats or blankets would have been relatively easy to produce – not necessarily involving much tailoring – and they could have been used flexibly, for example, as capes, when the situation required. As such, assuming the origins of clothing in plant fibres is a tempting alternative. The first animal-based clothing products may then have mimicked those made of plant materials. But to produce leather or pelt blankets demands deep knowledge of hide preparation and tanning techniques. To acquire the necessary skills and experience would have required some testing and experimentation, which could be more easily performed on small pieces of hide or fur. Smaller pieces of processed leather may have functioned as containers or bags for the transport of objects and liquids – necessary accessories for the highly mobile foragers that evolved in semi-arid environments.

The scenario outlined above would imply that ›clothes‹ – applying a broader definition of processed plant fibre products – would have been well in place before ancestral humans began to dress. This hypothesis aligns well with the genetic evidence for the early loss of body hair before the earliest hint at clothing production appears (see Rogers et al. 2004). Such an interpretation would also mean that the first clothing items, likely mats, blankets, containers, bags, or backpacks, may have developed in Africa, possibly far more than a million years ago, and that technologies expanded and diversified when confronted with the new challenges that early humans were facing in the mid-latitudes (cf. Gilligan 2010).

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Source of figures

1 author based on Pimenoff et al. 2017; Meyer et al. 2016; Prüfer et al. 2014; Prüfer et al. 2017; Endicott et al. 2010; Toups et al. 2011; d'Errico 2024; Gilligan et al. 2024; Herbert 2023, Lisiecki/Raymo 2005

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