UNIVERSITÀ
DEGLI STUDI
DI PADOVA

Head Office: Università degli Studi di Padova

DEPARTMENT OF BIOLOGY

DOCTORAL SCHOOL IN BIOSCIENCES
CURRICULUM: EVOLUTION, ECOLOGY AND CONSERVATION
XXXIV CYCLE

# THE DAWNING OF MAN: INTERROGATING MODERN HUMAN ORIGINS FROM AN EVOLUTIONARY AND EPISTEMIC PERSPECTIVE

Thesis written with the financial contribution of Fondazione Cassa di Risparmio di Padova e Rovigo, (CaRiPaRo)

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A thesis
submitted to the University of Padua
in fulfilment of the requirements for the degree of
Doctor of Philosophy

Università degli Studi di Padova

January 2022

*To have arrived on this earth as a product of a biological accident, only to depart through human arrogance, would be the ultimate irony.*

— Richard Leakey

# Abstract

This thesis aims at advancing evolutionary and epistemological knowledge of Middle and Late Pleistocene paleoanthropology, focusing on four main processes at the basis of cutting-edge research on modern human origins and evolution. These are the speciation of *Homo sapiens,* the transition to behavioural modernity, admixture with archaic hominin species outside Africa and human niche construction and global range expansion, here approached from the perspective of the current climate crisis.

First, an extended single-origin of *Homo sapiens* will be defended on evidential and evolutionary grounds, arguing that the paleoclimatic and paleoenvironmental context of Middle Pleistocene Africa likely favoured an allopatric speciation process from a widespread and diversified ancestral population. Then the thesis will move to the behavioural and archaeological side of the origin problem. I will analyse the evolution of the research agenda on "behavioural modernity", developing a philosophical account of "investigative *dis*integration" and criticizing Rubicon-based approaches that have not kept up with new standards of explanatory adequacy. I will then turn to paleogenomic research and discuss evidence of archaic admixture with respect to the taxonomic status of *Homo sapiens* and Neanderthals. I will approach the apparent conflict between molecular and morphology-based taxonomies from a diachronic perspective on lineage divergence and from an integrative perspective on different species conceptions and delimitation criteria, justifying distinct specific status on such grounds. Finally, I will frame anthropogenically-driven climate change as a niche construction process played at a global scale, having deep roots in *Homo sapiens* evolutionary history and long-term consequences that today require a counteractive response to prior actions to deviate from a potential evolutionary trap.

# Sommario

Questa tesi mira a contribuire allo sviluppo delle conoscenze evolutive ed epistemiche relative alla paleoantropologia del Pleistocene medio e superiore. Verranno analizzati quattro processi principali che stanno alle base della più recente ricerca sulle origini e l'evoluzione dell'uomo moderno: la speciazione di *Homo sapiens*; la transizione verso la "modernità comportamentale"; la mescolanza genetica con specie ominine "arcaiche" fuori dall'Africa; la costruzione di nicchia e l'espansione di areale a livello globale, qui affrontate dalla prospettiva della crisi climatica odierna.

Per prima cosa, difenderò un'origine singola *estesa* di *Homo sapiens*, sulla base di un'analisi delle evidenze attuali e delle conoscenze evoluzionistiche, sostenendo che il contesto paleoclimatico e paleoambientale del Pleistocene medio africano ha probabilmente favorito un processo di speciazione allopatrica a partire da una popolazione ancestrale distribuita sul continente e morfologicamente diversificata. Verrà poi affrontata la dimensione comportamentale e archeologica del problema delle origini. Analizzerò l'evoluzione dell'agenda di ricerca sulla modernità comportamentale, sviluppando un account filosofico definito di "*dis*integrazione investigativa" e criticando approcci basati su "Rubiconi" che non hanno tenuto il passo con i nuovi standard di adeguatezza esplicativa. Affronterò poi la ricerca paleogenomica e discuterò le evidenze di ibridazione con specie arcaiche in relazione al problema dello status tassonomico di *Homo sapiens* e dei Neanderthal. Analizzerò l'apparente conflitto tra tassonomie basate su dati molecolari e quelle basate su tratti morfologici da una prospettiva diacronica sul processo di divergenza di linee evolutive, e da una prospettiva integrata sui diversi concetti di specie e criteri di delimitazione, difendendo su tali basi una distinzione a livello specifico. Infine, contestualizzerò il cambiamento climatico di natura antropica come un processo di costruzione di nicchia giocato su scala planetaria, mostrandone

le radici profonde nella storia evolutiva di *Homo sapiens* e le conseguenze a lungo termine, che richiedono una risposta reattiva (*counteractive niche construction*) rispetto alle azioni precedenti per deviare dalla traiettoria verso una possibile trappola evolutiva.

# Acknowledgements

No research is done in a vacuum, nor should ever be. I am extremely grateful for all the assistance and support I received from professionals and colleagues during the past three years.

I am particularly indebted to my supervisor *Telmo Pievani* for offering me the opportunity of what I take to be a life-changing experience. Thanks for the patience, encouragement, guidance, and support. And thank you for teaching me the value of engaging in science communication as a constitutive part of the journey to becoming a better researcher and citizen.

My deepest gratitude goes also to my advisor and friend *Luca Pagani*, who never stopped challenging my thinking by helping me constantly question what I thought I understood (in the end it all paid off!). I am grateful for his invaluable input and support in navigating molecular anthropology and scientific literature and for all his professional advice. I have also greatly benefitted from the advice and collaboration with my other advisor *Giorgio Manzi*, who introduced me to the stimulating environment of the Paleoanthropological School of Perugia and deeply impacted my views and knowledge about physical anthropology.

My gratitude extends to the Department of Biology of the University of Padova, which offered a challenging but unprecedented habitat for a philosopher of science who cares about pursuing biologically and empirically constrained philosophical research. A few people stand out. Thank you to *Giuseppe Fusco, Mariella Rasotto, Andrea Pilastro, Clelia Gasparini*, *Ildikò Szabò* for feedback and suggestions along the way. My sincere thankfulness goes also to *Matteo Griggio*, whose presence we all miss and whose memory we treasure.

Despite the difficulties and limitations of the ongoing pandemic times, I have been lucky enough to spend three beautiful and stimulating months at Egenis, the Centre for the Study of Life Sciences (University of Exeter, UK). I cannot thank *Adrian Currie* enough: his creativity,

talent, sharp-mindedness and kindness are a continuous inspiration, both personally and philosophically.

I would also like to express my special thanks to those that shared part of this journey with me: present and past lab mates *Leonardo Vallini, Roberto Russo, Matteo Caldon, Max Saltori, Giacomo Moro Mauretto, Andrea Olmo Viola* and the colleagues of the Ph.D programme *Alexandra Glavaschi, Arianna Basile, Matteo Barbato, Arianna Dissegna, Federica Pirri, Livia Pinzoni, Emiliano Peretti, Davide Asnicar and Beniamino Tuliozi.*

A big thank you also to *Andrea Parravicini* and *Elena Canadelli* for advice, encouragement and cherished time spent together.

I cannot help but thank my partner *Francesco Suman* for giving me the extra motivation and strength and for his unwavering support and belief in everything I do.

Finally, cheers also to all those that have bothered asking me a question during a departmental presentation or at a conference talk or have spent some time commenting on a draft of mine. I deeply value every suggestion and criticism received over the past years.

# List of contents

# List of figures and tables

# Preface

This Ph.D. thesis aims at advancing evolutionary and epistemological knowledge arising from the study of Middle and Late Pleistocene paleoanthropology, with a focus on both anatomical and behavioural origins of modern humans (*Homo sapiens*) and their relationship with coeval hominin species (in particular, with *H. neanderthalensis*). These topics are explored throughout four first-author papers that have been written at different stages of my Ph.D. programme, here presented in logical and narrative order, rather than in the chronological order in which they have been published or submitted, and reformatted for consistency of style (a list is provided below).

Each paper will comprise a separate chapter and will cover one of the four main points of focus of the current thesis:

1. The speciation of *Homo sapiens* in Africa (Chapter 2);
2. The transition to “Behavioural Modernity” (Chapter 3);
3. The implications of the evidence of admixture between archaic and modern humans outside Africa (Chapter 4);
4. Human niche construction and its relationship with the current climate crisis (Chapter 5).

The paper from Chapter 5 has been published in the journal *Biology and Philosophy*, while the one from Chapter 3 has been accepted for publication in *Synthese*. The remaining two are currently at different stages of the peer-review process at scientific journals: the review paper from Chapter 2 is a revised version resubmitted to *Evolutionary Anthropology*, while the point-of-view paper from Chapter 4 is currently under review at *Systematic Biology*. Although other publications have been produced during the three-year programme (a complete list is provided in the Appendix), for evaluation purposes I have decided to include those for which my research work, writing and ideas have been undeniably substantive, *i.e.* first-author papers only.

Each paper constitutes a self-contained argument, with its own introduction and conclusions, and can in principle be read in any order the reader might choose. However, I would recommend starting with the introduction, as it is intended to provide the fundamental background and rationale of the research, that each chapter instantiates in a different manner. Although I have made efforts to improve the coherence of the thesis while avoiding redundancies in the introduction and the conclusions, some small degree of overlapping content is to be expected.

Moreover, I expect the research work presented in this thesis to reflect an interdisciplinary academic background. Although my training has been in Philosophy both during my undergraduate and master's years, I have pursued a Ph.D. in the Philosophy of Biological Sciences at the Department of Biology of the University of Padua, thus receiving a hybrid education across philosophy, paleoanthropology and evolutionary biology, and being exposed to scientific research in its everyday practice. This has inevitably shaped my approach, which is largely a bottom-up one: I try to bring to the surface epistemological aspects from the folds of the science of human evolution, starting from an in-depth study of the primary, updated literature.

For each chapter, each point of focus will be approached through specific research questions (a more detailed discussion will be provided in paragraph 1.3 of the Introduction), ranging from evolutionary approaches that draw strongly on the empirical and evidential details of the debates at hand, to more theoretical and epistemological perspectives. For instance, as regards the speciation problem of *Homo sapiens* in Africa (Ch. 2), in light of recent advances and discoveries from the last few years, I will ask how the current modern human origins debate can be reconciled with evolutionary knowledge and theory, which is often not explicitly addressed in paleoanthropological literature. The final chapter (Ch. 5) is to be read as an epilogue of the thesis journey through key stages and processes that led to humankind, exploring the evolutionary roots and long-term implications of our niche construction abilities.

All the figures and tables have been renumbered according to the order in which they appear in this thesis.

The list below summarizes information about the manuscripts on which the thesis is based:

- **Meneganzin A**., Pievani T., Manzi G. Pan-Africanism vs single-origin of *Homo sapiens*: putting the debate in the light of evolutionary biology. [Status: Revision Submitted]. *Evolutionary Anthropology*.
- **Meneganzin A**., Currie A. Behavioural modernity, investigative disintegration and Rubicon bias. [Status: in press]. *Synthese*.
- **Meneganzin A**., Bernardi M. Were Neanderthals and *Homo sapiens* 'good species'? [Status: Under review]. *Systematic Biology*.
- **Meneganzin A**., Pievani T., Caserini S. (2020) Anthropogenic climate change as a monumental niche construction process: background and philosophical aspects. *Biol Philos* 35, 38. https://doi.org/10.1007/s10539-020-09754-2

Finally, although all chapters are based on co-authored manuscripts and the arguments and ideas equally belong to my co-authors, in the introduction and the conclusions I have elected to use "I" as a self-referential pronoun, for the sake of clarity, while I have kept the "we" pronoun in Chapters 2-5. Here, however, I alone am to be held responsible for any shortcomings or mistakes the reader might find.

# 1.

# Introduction

## 1.1 The historical science of our origins

The question about the origins and evolution of *Homo sapiens*, and about how we know what we think we know, is more topical than ever before. Although the issue has been debated for several decades (see Stringer 2002, 2016), it has not lost any of its relevance today in virtue of what I take to be two main interrelated factors: (i) constitutive epistemic features of paleoanthropological investigation and (ii) recent expansions of the evidential and methodological basis, frequently changing the terms and sometimes the very nature of the debate. In this introduction, I will cover these factors in order and highlight how they feed into the origin problem, before detailing the scope, research questions and structure of the thesis.

The study of human evolution epitomizes the peculiar epistemic conditions that characterize many historical sciences (Cleland 2002, 2011; Gould 2002; Turner 2007, 2014; Currie 2018, 2019). Paleoanthropologists target phenomena in the deep human past that are not amenable to the luxury of experimental investigation and are frequently at an impressive epistemic distance from the evidence at hand, *i.e.* often degraded and incomplete material remains.

Indeed, and crucially for the central worry of this thesis, a central resource of data for much work on modern human origins still comes from the fossil and the archaeological record. This means engaging with the opportunities and constitutive limits of such records. Fossils don’t speak for themselves and much debate on the origin of *Homo sapiens* hinges on the interpretation of key but ambiguous fossil remains in contexts characterized by a marked scarcity of information, such as the Late Middle Pleistocene African fossil record (as we shall see). Also, disentangling issues of preservation bias in material culture from evolutionary mechanisms that predict patchy and mosaic-like outcomes is critical for addressing the question of how behavioural and cultural complexity evolved.

Further, as it is the case for other historical sciences, the science of human origins works with a multiplicity of evidential streams, ranging from physical anthropological and archaeological data to modern and paleo genomes, to paleoenvironmental and paleoclimatic reconstructions. Paleoanthropology is at its very core a multidisciplinary enterprise. The convergence or concordance of multiple lines of evidence on the same result or hypothesis (consilience; Forber and Griffith 2011) is generally considered an important epistemic *desideratum* and indeed constitutes a central source of support for historical reconstruction. However, prior to waving together different evidential threads, fundamental questions need to be asked about what kinds of evidence are relevant for the question at hand, whether discordance should be valued as informative and if so, how should it be dealt with.

Moreover, the mobilization of new data as evidence – or even putting old data to work in new ways (Wylie 2017) – requires drawing on background knowledge that provides the relevant connecting links in inferences from empirical premises. These forms of “inferential scaffolding” (Chapman and Wylie 2016; Currie 2018) underwrite the effectiveness of the historical sciences in overcoming the vagaries of trace survival and securing the prospect of research progress. Human origins research can benefit from a vast and heterogenous array of background knowledge to formulate hypotheses about human past – first and foremost, evolutionary biology. However, the way evolutionary knowledge is recruited to inform paleoanthropological traces (be they fossil or genetic) is not straightforward and the permeability of paleoanthropological practice by evolutionary theory, somewhat counterintuitively, has a tortuous history (Delisle 2012).

But the study of human evolution has obviously an additional feature, which stems from our unique predicament (and a source of further challenges) as both subject and object of study. The science of human origins is about reconstructing our evolutionary history, disentangling our intertwined ancestry and understanding our relationship with other coeval hominin and human forms. This means constantly mitigating a suite of common biases that may arise when writing history from the winners' perspective.

All the above aspects are instantiated in various forms by the main chapters of this thesis, albeit through discussions that will zoom in on cutting-edge scientific research and will often foreground empirical detail. In what follows, I will discuss the main sources of disciplinary change over the past ten years that motivate the current research before turning to the scope and aims of my thesis.

## 1.2 Challenges and opportunities from the last decade

Although frequently regarded as a discipline hopelessly hampered by ungenerous data and sometimes by excessive narrative freedom (Landau 1993), looking at the past ten years only, human evolutionary research has advanced considerably. The epistemic limitations on the retrievability of past events (seen in 1.1) that paleoanthropology shares with other historical sciences are not *static* limitations. Major methodological and empirical expansions have reshaped our epistemic reach into hominin evolutionary past and have offered a much more diverse and dynamic image of our origins. This creates new theoretical challenges and offers now more than ever fertile fields of inquiry from a philosophical and evolutionary perspective. In this section, I'll provide an overview of the developments on which the chapters of the thesis draw upon.

### *1.2.1 Uncovering the past with the technology of the future*

While it is generally true that dead men don't tell tales, paleoanthropologists have sharpened their techniques to make them talk and extract as much information as possible from the available evidence. The study of human evolution has enriched its methodological arsenal at different levels, benefitting from advances in geometric morphometrics and virtual anthropology, allowing for a non-invasive and numerical approach towards hominin remains and their variation in shape. Moreover, methods like ZooMS (Zooarchaeology by Mass Spectrometry, cfr. Douka et al. 2019) have made it possible to exploit collagen and its slow evolution as a molecular barcode to identify large numbers of morphologically undiagnosed bone fragments.

However, one of the major lines of evidence to have entered the scene comes in an obvious way from the so-called "paleogenomic revolution". Advances in extraction methods and the application of high-performance sequencing techniques to the study of ancient DNA (aDNA) have made it possible to analyse complete genomes of extinct hominins. This has yielded seismic shifts in our understanding of human evolution, continuously reshuffling old conundra and related explanatory narratives. This process is clearly exemplified by an increasing understanding of the role played by hominin admixture and interbreeding in modern human origins and by our ability to quantify it.

The possibility that *Homo sapiens* exchanged genes with other hominin forms, although a topic of fierce debates (Tattersall and Schwartz 1999), was expected from fossil and archaeological remains and doesn't *per se* represent a biological scandal. Today we're the only representatives of our genus walking the planet, but this solitude is a very recent feature of our evolutionary history. Taking a bar graph with conservative estimates of the temporal ranges of hominin

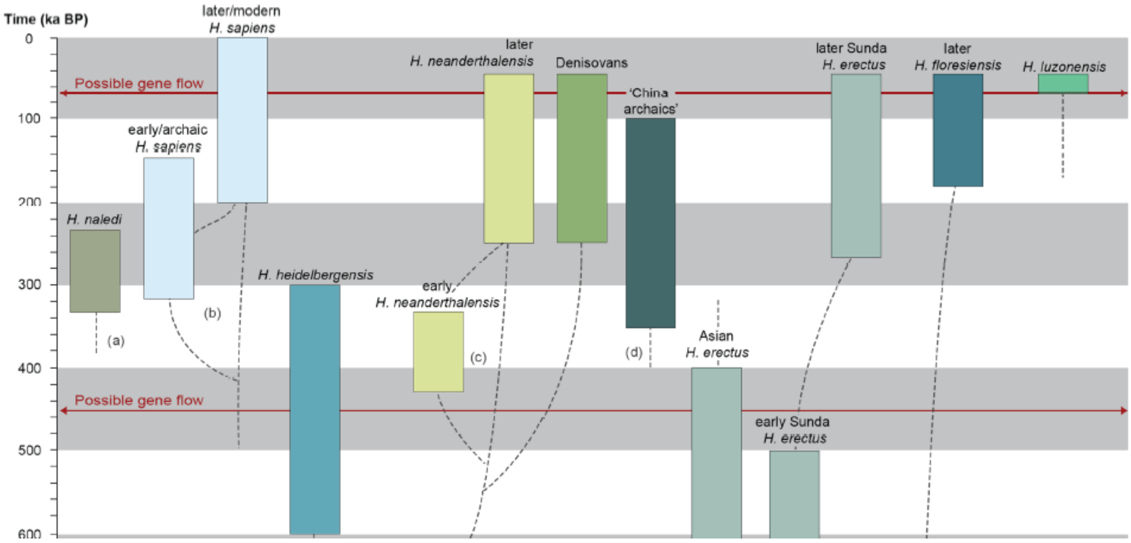

**Figure 1. Schematic diagram of the inferred age ranges of hominin lineages during the last 600.000 years.** Retrieved and adapted from Galway-Witham, Cole and Stringer (2019).

species (Wood & Boyle 2016, Galway-Witham, Cole & Stringer 2019) and drawing parallel horizontal lines, we'll immediately notice a temporal overlap among *Homo sapiens* and at least five other hominin species, some of which have been named only in the past few years (*Homo neanderthalensis*, Denisovans, *Homo erectus, Homo floresiensis*, *Homo luzonensis*). Where also spatial overlapping occurs, coexistence takes on evolutionary significance, meaning the possibility of interaction, through genetic and cultural exchange, or competition (see Fig. 1).

In particular, paleogenomic data have revealed a rich scenario of interactions among us and our extinct evolutionary cousins, the Neanderthals. It is widely known that non-African populations share around 2% of their genetic makeup with the Neanderthals (Green et al. 2010). Other episodes of interbreeding have been recently identified from early *Homo sapiens* genomes, with differing contributions to later modern human populations (Hajdinjak et al. 2021; Prüfer et al. 2021). Moreover, through genetic analyses of small bone fragments discovered in a cave in the Altai Mountains (Siberia), the Denisovans have been identified as a new hominin population, which crossbred both with the Neanderthals (Slon et al. 2018) and our species, leaving a genetic signature of those encounters among south-east Asian populations (4-6% of DNA in humans currently living Papua and New Guinea, Australia and Melanesia; Reich et al. 2010).

These analyses have yielded important questions (Galway-Witham and Stringer 2018). First, one of the tenets of the current consensus theory on modern human origins – the Recent Africa Origin theory (RAO) – suggesting that in its expansion outside Africa, *Homo sapiens* would have replaced all archaic human groups without any interbreeding, demanded revision. Second, and as it'll be extensively discussed in Chapter 4, immediate questions have been raised on the taxonomic status of hominins for which evidence of interbreeding was established and on the impact of such evidence for the topology of human phylogeny.

Moreover, other aspects of RAO have started to be questioned based on new fossil discoveries, such as the exact time and place of the emergence of *Homo sapiens* within the African continent, to which we'll turn now.

### *1.2.2 New bones from Africa*

Until very recently, the earliest African fossils attributed to our species came from regions of East Africa, more specifically from Ethiopian sites, dated not older than 200.000 years (ka). Claims shedding doubts the "single-origin" version of RAO – *Homo sapiens* evolving from a single population or region in Africa – have been significantly prompted by new findings from the site of Jebel Irhoud, in Morocco (Hublin et al. 2017).

The material, dated to more than 315ka (Richter et al. 2017) and presenting a complex and taxonomically ambiguous combination of ancestral and derived traits, was received as documenting the earliest forms of *Homo sapiens* in the continent, pushing back the appearance of our kind by more than 100ka. Moreover, the fossils, coming from a region that was not on the radar as a top candidate for the cradle of humankind, were described as evidencing that the evolutionary process behind the emergence of our species involved the whole African continent. Proponents of what is now known as the “pan-African” scenario of our origins (Scerri et al. 2018, Scerri et. 2019) argue that a polycentric emergence of *Homo sapiens* is now supported by different and independent lines of evidence (thus invoking a consilience argument), including the morphological diversity of Pleistocene human fossils, genetic studies, and the archaeological record.

Remaining on the fossil side, deciphering the diversity of the African Late Middle Pleistocene record is crucial for advancing our understanding of the origin problem. The marked phenetic variability exhibited by the African fossils (Mounier and Lahr 2019) even encompassed the presence of different *Homo* lineages in the continent, like *Homo heidelbergensis,* with the recently redated cranium of Broken Hill to 299 ka (Grün et al. 2020) and the remains of bizarre *Homo naledi,* dated 335–236 (Berger et al. 2017). Fundamental questions then arise on the taxonomic interpretation of the Jebel Irhoud material (as we shall explore in detail in Chapter 2), especially if used to corroborate the interpretation of other fragmentary, poorly dated and equally ambiguous remains (like those from Florisbad, in South Africa, Grün et al. 1996).

Moreover, the integration of other lines of evidence requires first ascertaining that they all point to the same target and are not compatible with alternative readings. Further, and crucially for a discipline characterized by evidential scarcity, new traces are rare commodities, but it’s only through various layers of interpretive scaffolding that these are constituted as evidence. Interrogating those scaffolds and putting the data against overlooked theoretical frameworks (like, as I shall argue for this specific debate, evolutionary knowledge on speciation processes) is key to understanding whether new data can be integrated into prior explanatory models or if the models need to be discarded.

### *1.2.3 The archaeological gaze on behaviour and culture*

Besides technological advances and debates ignited by new fossil discoveries, the last years of research on human origins have seen major reorientations also in the archaeological domain. These have been equally driven by empirical and theoretical developments and have followed two main trajectories: (i) the consolidation of explanatory models shifting away from broad temporally and spatially unitary narratives of how humans attained "behavioural modernity" and (ii) an increased appreciation of behavioural and cultural complexity among non-*sapiens* species, notably the Neanderthals.

Let's start with the first point. The concept of behavioural modernity and the related research are deeply rooted in debates that have spanned more than thirty years. The notion itself is linked to what archaeologist Colin Renfrew has termed "the sapient paradox" (Renfrew 1996, 2008). The puzzle stems from an apparent temporal mismatch in the material record between the emergence of the anatomical apomorphies defining our species (anatomical modernity, now set around 200-300 ka), and the onset of a broad-based surge in human material culture and sophisticated behavioural expressions, after 100 ka (Henshilwood and Marean 2003).

What behavioural modernity actually *is* and the models used to explain it have undergone substantial changes since Renfrew's formulation of the paradox. First, what should be considered an archaeological signature of the phenomenon – *i.e.* how the hallmarks of "what makes us human" should be translated into material traces – has been periodically rethought to address problems of empirical derivation (the context-specificity of traits), ambiguity and taphonomic bias. So have been the models explaining the signatures, together with the proposed mechanisms for the transition, and the timing of the transition itself. From revolution scenarios targeting the European Upper Paleolithic and based on hardwired genetic or biological triggers, the debate has now shifted to the interplay among biological and cognitive prerequisites and demographic and sociocultural factors in local environmental contexts to explain the evolution of cultural repertoires, and the stabilization and expansion of the human niche (D'Errico and Stringer 2011; D'Errico and Banks 2013, Kissel and Fuentes 2018, Sterelny 2021).

Part of this reorientation has been possible thanks to a profound re-appreciation of the depth and complexity of the African archaeological record of the Middle Stone Age (McBrearty and Brooks 2000) but also of other regions, like the Near East and Europe, that show an array of innovations preceding the arrival of modern humans in those territories (reviewed in Colagè and d'Errico 2018).

In particular, and this is the second point mentioned above, compelling new evidence has shown that many indicators of behavioural modernity are also displayed by anatomically "archaic" populations, and significantly by the Neanderthals (although with varying degree and form; d'Errico et al. 2003, Villa & Roebroeks 2014). If the concept was initially employed to mark a significant adaptive and cognitive disjuncture between *Homo sapiens* and our closest hominin relatives, expansions and re-readings of the record have cast serious doubts on the idea that behavioural modernity should be treated as a uniquely *sapiens* story. Although this does not immediately commit research to much debated " Neanderthal indistinguishability" claims (Wynn et al. 2016), the increasing appreciation of the *mosaic* nature of the transition (Foley 2016, Parravicini and Pievani 2019), taking place across branches of recent hominin phylogeny, indeed provides a much more complex, temporally and spatially patterned framework of how hominins became human.

Altogether, these issues delineate a radical reshaping of the research agenda and investigations of behavioural modernity. The very term "investigation" draws its etymological origins from the latin word "*vestigium*", meaning vestige, footprint or trace. What happens then to investigations when new vestiges appear and our strategies for reading the old ones change?

According to some, if recent models are on the right track, Renfrew's paradox should no longer be considered a paradox at all (Sterelny and Hiscock 2017). Shea (2011) suggests that the changes have been of such magnitude that we should get rid of the concept of behavioural modernity *in toto* (Shea 2011). As we shall explore in chapter 3, the debate offers a fertile terrain for understanding the dynamics and drivers behind the evolution of research agendas on deep human past.

## 1.3 Scope and driving questions of the thesis

In this section, I will pull together the threads delineated in the previous two sections and illustrate more in detail the approach, the driving questions and contributions of each chapter.

Although adopting different angles and approaches, the four chapters focus on distinct processes within the Recent African Origin framework. These are the speciation of *Homo sapiens* (Chapter 2), the transition to behavioural modernity (Chapter 3); admixture with archaic hominin species outside Africa (Chapter 4); human niche construction and global range expansion, with implications for the current climate crisis (Chapter 5). This thesis then can be schematically conceived as a collection of arguments aimed at shedding light on a cluster of interrelated processes and issues that are crucial for understanding the origins of *Homo sapiens*.

Methodologically speaking, some aspects will be common to all chapters, while others will differ. On the one hand, each chapter of the thesis will start with, or will contain, a critical analysis of relevant scientific evidence and of points of contention in scientific debates. This will often mean engaging closely with empirical details, putting them in order, and making sense of technical aspects of paleoanthropological research. While this does not *per se* qualify as philosophical analysis in the conventional sense, it nonetheless provides the bedrock for the empirically-driven philosophical research I like to pursue. On the other hand, and starting from this basis, some chapters will proceed with evolutionary scenario building (Chapter 2), proposing integrative solutions that, in my view, best fit available theoretical and empirical knowledge. This however is only possible after a reflection on issues of methods, evidence and theory. On the other hand, chapters like Chapter 3 will offer a more evident philosophical analysis of dynamics of scientific research on the deep past, introducing new accounts and concepts to capture changes in the epistemic structure of investigations. Chapters 4 and 5 will bring evolutionary theory and systematics to bear on evidence synthetised from various fields, with the aim of bringing to the surface otherwise neglected implications, or reformulating (and hopefully dissolving) recurring debates.

Let us turn now more specifically to the driving research questions and contributions of the thesis. In Chapter 2 I will ask to what extent is the biological evolution of *Homo sapiens* representative of patterns and problems in evolutionary biology. In light of recent suggestions of a pan-African emergence of *Homo sapiens*, ignited by discoveries at Jebel Irhoud site, I will try to reframe the debate as an evolutionary problem about *speciation*, therefore tackling the emergence of derived characters of our species. This is motivated by a general lack of evolutionary contextualization and discussion in leading paleoanthropological publications on human origins. Palaeontologist Elizabeth Vrba has long emphasised the necessity to study hominins in their wider biotic and environmental context in order to grasp the role of environmental stimuli in hominin origins, according the theory of evolution more prominence than has been the norm (Vrba 2015). In chapter 2 then, before critically reviewing the evidential threads on which the “Single-Origin” and the “pan-African” models are based, and casting doubts on the interpretation of some of them, I will suggest a synthetic position within the debate, describing a speciation process that is consistent with the pronounced changes in climate (and thus levels of connectivity among populations) in Middle Pleistocene Africa.

This also speaks to a common, pessimistic accusation addressed to paleoanthropology – it appearing to be trapped in endless and recurring debates (Kurten 1981). And indeed, the current debate on modern human origins reproposes aspects of the old Multiregional vs. Recent African Origin contention (Stringer 2014). Bringing the debate back on the evolutionary track is crucial to make new incoming evidence feed into a progressive understanding of our speciation process.

Chapter 3 will ask about the nature of changes in our understanding of behavioural modernity phenomenon and the related consequences for archaeological practices and approaches to categorization. This will be framed as a form of "investigative *dis*integration" driven by a radically different conception of the phenomenon, which in turn leads to shifts in empirical and theoretical regimes. This chapter will aim at analysing an underexplored dynamic of progress in scientific research on the deep past. While much work has understandably focused on how research stabilises and how new data, collected from a variety of fields, are integrated into available models and problem agendas, interesting forms of disintegration may foster new research avenues, with new leading questions, concepts, and approaches. I will show how this has unfolded in the case of behavioural modernity and how new criteria of explanatory adequacy fail to be met by still surviving practices centred on "Rubicon expectations" – *i.e.*, practices that depict the evolution of modern behaviour as a demarcation problem.

Chapter 4 will move outside of Africa and will tackle the vexed question of whether *H. sapiens* and Neanderthals should rightfully be considered separate species. Although I distinctly remember promising myself to resist the temptation of writing a paper on species delimitation during the first year of my Ph.D., the evolution of the epistemic context, persistent nomenclature inconsistencies in the literature and evolutionary implications behind hominin taxonomic status have offered valid reasons for a change of mind. Indeed, there's hardly another paleobiological context that can benefit from distinct sources of evidence other than morphological data to assess species boundaries, let alone ancient molecular data. The chapter first begins with a review of the evidence of archaic interbreeding and discusses its impact. Then, the issue of species status and the apparent conflict between molecular and morphology-based taxonomies is approached from a diachronic perspective on lineage divergence, highlighting how different taxonomic properties are expected to arise at different points in time, and from an integrative perspective on different species conceptions and delimitation criteria (following de Queiroz 2007).

Chapter 5, despite being one of the first papers to have been written and published during my Ph.D, serves as an epilogue – a look into the future of our species, informed by its evolutionary past and journey. Here I will ask how evolutionary theory can frame and inform *Homo sapiens*' impact on global biodiversity and climate. More specifically, I will argue that anthropogenically-driven climate change meets the criteria for a niche construction process (Matthews et al. 2014), affecting the selective pressures and evolution not only of other organisms, but our own. Although niche construction is usually conceived as an adaptive process – an organism moulding spaces to survive and thrive in them – impoverished ecosystems and an altered climate are now impacting negatively on human health and wellbeing too. Therefore, I will show that our transformative capacities, deeply rooted in the evolutionary history of *Homo sapiens*, are now taking the form of an evolutionary trap for ourselves, requiring us to produce an adaptive response – played at the cultural level – to the changes produced by our own activities.

Overall, then, this thesis aims at contributing to the understanding of human origins by weaving together analyses on the epistemic standing of paleoanthropological research and through an evolutionary framing of current evidence and debates.

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# 2.

# The speciation of *Homo sapiens*

## Pan-Africanism vs single-origin of *Homo sapiens:* Putting the debate in the light of evolutionary biology

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## Abstract

The scenario of *Homo sapiens* origin/s within Africa has become increasingly complex, with a pan-African perspective currently challenging the long-established single-origin hypothesis. In this paper, we review the lines of evidence employed in support of each model, highlighting inferential limitations and possible terminological misunderstandings. We argue that the metapopulation scenario envisaged by pan-African proponents well describes a mosaic diversification among late Middle Pleistocene groups. However, this does not rule out a major contribution that emerged from a single population where crucial derived features – notably, a globular braincase – appeared as the result of a punctuated, cladogenetic event. Thus, we suggest that a synthesis is possible and propose a scenario that, in our view, better reconciles with consolidated expectations in evolutionary theory. This indicates cladogenesis in allopatry as an ordinary pattern for the origin of a new species, particularly during phases of marked climatic and environmental instability.

## Keywords

Anagenesis *vs.* cladogenesis; Mosaic evolution; Pan-African hypothesis; Punctuationism; Single-origin hypothesis; Speciation of *Homo sapiens*

## 1. Introduction

The emergence of *Homo sapiens* has sometimes been defined as a "recipe for frustration" (Foley et al. 2016), or an "unsolvable puzzle" (Batini and Jobling 2011). Indeed, the story of our origins is to date ever more complex and no less elusive, as the available data do not seem in many respects to have sufficient resolution to discriminate among alternative scenarios. Here we propose to rethink the origins debate as a problem about *speciation* – *i.e.*, the tempo and mode of how our species came to be – focussing on the process behind the appearance of key autapomorphies in the African fossil record. We argue that a perspective coherent with evolutionary biological knowledge can be valuable when combined with skeletal, paleoenvironmental, archaeological and genomic data, thus reducing the apparent underdetermination of hypotheses by current evidence (e.g., Bergström et al. 2021).

Today’s picture on how *Homo sapiens* evolved from its ancestors (hereinafter referred to as the "last common ancestor" shared with Neanderthals and Denisovans, or LCA) of the Middle Pleistocene (now Chibanian; cfr. Hornyak 2020) remains nested in the Recent African Origin (RAO) model, which since the last decades of the XX century has withstood the confrontation with multiregional models (MRE; Aiello 1993, Stringer 2002, Manzi 2012). First suggested by patterns of morphological variation in the fossil record (Howells 1973, Smith and Spencer 1984, Stringer and Andrews 1988, Mellars and Stringer 1989) and by coalescence time estimates from mtDNA present diversity (Cann et al. 1987), our African origin is corroborated by a multiplicity of evidential strands. These include the earliest and uncontroversial *Homo sapiens* fossils in Africa (White et al. 2003, McDougall et al. 2005, Stringer 2016) as well as studies on human genetic diversity (Ramachandran et al. 2005, Mallick et al. 2016), which show that diversity is greater in Africa than in any other region of the world, decreasing with increasing geographic distance from this continent. The fact that small portions of the present genome of *Homo sapiens* are of Eurasian “archaic” origin (*i.e.* introgressions from Neanderthals, Denisovans and other deeply divergent lineages; Green et al. 2010, Reich et al. 2010) rejects the strictest versions of RAO – *i.e.*, the scenario of full replacement – but it does not provide support to the multiregional and long-standing gene flow claimed by MRE (Holliday et al. 2014, Stringer 2014, Wolpoff et al. 1994).

Now that research on modern human origins has shifted its focus to what happened *within* the African continent at the dawn of our species, some scholars suggest that a continent-wide process could have occurred during the second half of the Middle Pleistocene, leading to a hypothesis commonly referred to as "pan-African" (Bergström et al. 2021, Stringer 2002, Hublin et al. 2017, Scerri et al. 2018). This stands in contrast to the idea, implicit in some of the early RAO formulations, of a cladogenetic and punctuated (*sensu* Eldredge & Gould 1972, Gould & Eldredge 1977, Lieberman & Eldredge 2014) event of speciation, with the subsequent dispersal of *Homo sapiens* in and outside Africa.

In this paper, we critically review the two latter positions from the perspective provided by general principles in evolutionary biology. We suggest that, when a "*simple* single-origin" (i.e., localized evolution of the entire "package" of modern traits) is excluded, the actual alternative is between the pan-African scenario and an "*extended* single-origin", which is viewed here as the result of pre-modern and post-modern phases of mosaic evolution of traits, interposed with the crucial change represented by the appearance of a new architecture of the neurocranium (*i.e.*, globularity), with its underlying ontogenetic mechanisms and determinants.

## 2. Single-origin hypotheses

### *2.1 Contenders for the Cradle of Modern Humans*

Different bodies of evidence have been used to support the view that our species evolved within a single ancestral population, which must be traced back to a localized region in Africa. Based on different tangles of independent lines of evidence, an eastern and a southern birthplace for *Homo sapiens* have both been proposed (McDougall et al. 2005, Henn et al. 2011, Henn et al. 2018, Rito et al. 2019, Chan et al. 2019).

The East African system of rift valleys, with a complex topographic and ecological structure favouring niche subdivision and therefore promoting diversity (Foley 2018), has always been in the spotlight of human evolutionary research, offering a wealth of paleoanthropological and archaeological discoveries, thus becoming the top candidate as "cradle of humankind" (McDougall et al. 2005, Stringer 2003). The patchy sets of environments and the variety of biomes have been shown to house hotspots of endemism in many vertebrate taxa (particularly amphibians, birds and mammals; Riggio et al. 2019). Thus, a sort of "East side story" (Coppens

1994), as proposed for the origin of hominins, has also been suggested for the emergence of our species (Ray et al. 2005, Liu et al. 2006, Manzi and Di Vincenzo 2013).

The biological evidence that is usually cited to support an eastern birthplace for *Homo sapiens* is twofold. First, the earliest accepted fully modern human skulls have been found at Ethiopian sites, in the Kibish Formation of Omo Valley (McDougall et al. 2005) and at Herto in Middle Awash (White et al. 2003), respectively dated to 195 and 160 ka. Omo Kibish 1 and Herto 1 specimens are endowed with a modern cranial morphology, which is usually held to consist in a high, rounded and voluminous vault, and a small, gracile face, with evidence in Omo 1 of a canine fossa and mental eminence (Day and Stringer 1991, Stringer 2016), therefore providing East Africa with the strongest case for human phenotypic evolution. These representatives of anatomically modern humans were still more robust than modern-day ones, and some specimens show a strong supraorbital torus, although dived into central and distal parts (Stinger 2016). The African middle to early late Pleistocene fossil record is relatively sparse and the sedimentary basins of East Africa, whose material evidence dominates the record, take advantage of particularly favourable conditions of fossilization. While this represents an important source of bias that must not be overlooked when drawing regional inferences about the evolutionary dynamics that shaped diversity in the continent, some still argue for a major role of East Africa as a crucial area of endemism for its particular biogeographical context (Lahr and Foley 2016).

Second, the above-mentioned datings sat well with the pioneering genetic studies of mitochondrial DNA (mtDNA) of different modern populations worldwide. Studies performed in the late ‘80s estimated that the most recent matrilineal common ancestor (mt-MRCA) – the so-called “mitochondrial Eve” – dated to 200 ka and lived in Sub-Saharan Africa (Cann et al. 1987). Although the original research displayed several analytical limitations, this estimate has been confirmed by later research, with new calibration points for the mitochondrial clock and revised substitution rates at about 120-197 ka (Fu et al. 2013, Soares et al. 2016; but see discussion below for caution on the population history questions that can be addressed with single-locus phylogenetic trees).

Not only Ethiopia has claimed to be the crucible of humankind. A southern African origin has also been proposed based on genomic diversity (Henn et al. 2011, Rito et al. 2019, Chan et al. 2019), archaeological evidence (Marean et al. 2007, Henshilwood et al. 2009, Wilkins et al. 2021), as well as on the capacity of providing stable resources and refugia during the marine isotope stage 6 (MIS 6; Marean 2011).

African hunter-gatherers show the highest levels of genomic diversity in the world, encompassing components of variation that are not found in any other African population (Henn et al. 2011). Chan and colleagues (2019) claimed to have pinpointed the exact place of origin of anatomically modern humans in Makgadikgadi–Okavango palaeo-wetland of today's northern Botswana, south of the Zambesi basin, around 200 ka. Their conclusion is derived from the structure of the inferred phylogenetic tree based on 1217 samples of mtDNA (of which 198 were newly generated) of rare and deep-rooting L0 haplogroup, which is highly frequent in the Khoe-San people. The research has attracted widespread criticism, the most serious being the use of a phylogenetic tree at a single non-recombing locus, which is a random outcome of the genealogical process, to make inferences about population history (see Schlebusch et al. 2021 and *preprint* by Ackermann et al. 2019). Moreover, the implicit assumption that the present-day geographic location of a population has remained substantially unchanged for tens of thousands of years is controversial and needs to be supported by fossil and ideally aDNA evidence, that are dramatically scarce for such deep-time periods, and which would contradict results from studies on Holocene populations (Schlebusch et al. 2021).

From an archaeological perspective, south Africa hosts early and important evidence for the emergence of key elements of modern human behaviour, such as the use of marine resources, pigments and abstract imagery (Rito et al. 2019, Marean et al. 2007, Marean 2011, Henshilwood et al. 2009, Wilkins et al 2021). However, archaeological evidence should be handled with care in this context, both because makers are never identifiable with certainty (especially in settings of multiple overlapping species and populations) and because cultural dynamics do not need to follow the same patterns of evolution and transmission of biological traits, although biological and cultural dimensions can strongly interact with each other (Richerson and Boyd 2008). Put another way, the signature of our modern behavioural evolution does not need to be confined to southern Africa, with the initial appearance of the Later Stone Age (Ackermann et al. 2016). In fact, a more intricate and pluralistic scenario has been recently suggested for behavioural modernity, under which key cultural innovations appeared and disappeared in an asynchronous and polycentric fashion not only within the African Middle Stone Age – the earliest evidence of which is found contemporaneously around 300-250 ka across much of the continent – but also in the Eurasian Middle Paleolithic, involving multiple lineages (D'Errico and Stringer 2011, D'Errico and Banks 2013).

### *2.2 The evolutionary background of RAO*

Despite the methodological and empirical limitations that make it difficult to reach a regional scale resolution in the analysis of our evolutionary past, the idea of a single origin draws historically its strength from a well-known legacy in evolutionary biology. According to the allopatric model of speciation, famously championed by Ernst Mayr, speciation is most likely to occur in small, peripheral populations that have geographically separated from the larger parental population (Mayr 1942, 1963). At the micro-evolutionary level, small population are majorly susceptible to quick evolutionary changes (by genetic drift or natural selection) as they contain less genetic variation and thus are less stable than large ones. Extending Mayr's geographical perspective on speciation, Gould and Eldredge derived a macroevolutionary mechanism for variability in rates of evolution, the “punctuated equilibria” theory (Eldredge and Gould 1972, Gould and Eldredge 1977), arguing that speciation is a rare event that punctuates a system in apparent equilibrium (or "stasis"). According to such view, frequently the onset of new species is a (geologically speaking) rapid process, and new species are to be found in narrowly limited regions, geographically distant from (or isolated with respect to) the area of their ancestors.

Inevitably, these ideas exerted – and still do – an indirect but significant impact on paleoanthropological research (Eldredge and Tattersall 1982, Pievani 2012, Tattersall 2013) having long oriented the appraisal of the diversity evident from the available fossil record and providing an evolutionary framework for the Recent African Origin model (whereas the earlier and now refuted Multiregional hypothesis fits comfortably the phyletic gradualism promoted by the standard evolutionary Modern Synthesis; Pievani 2015). Central for the single-origin hypothesis is the idea that evolution, considered as change across time, starts essentially in space, *i.e.* in geographical locales, mostly during periods of ecological instability. We will argue that this framework, when not confused with extreme oversimplifications, still proves informative in the context of the evolution of *Homo sapiens*.

Elizabeth Vrba’s contributions to mammalian palaeontology and theory of macroevolution have provided milestones in understanding the role of environmental disruption in prompting both extinction and speciation processes (“turnover pulses”), with origination of new lineages being highly favoured by fragmentation of habitats and resulting opportunities of diversification for allopatric populations (Vrba 1980, 1992, 1993). This perspective acquires significance if the origin of our lineage is to be set within a phase of strong environmental changes, particularly accentuated from MIS 6 (cfr. Jones and Stewart 2016, but clearly having deeper roots, as we will argue) that might have well affected landscape geomorphology and consequently population sizes, interconnectedness and distribution.

There is no doubt that current debate has added new depth and complexity to the narrative of modern human origins, as we shall explore in the following sections. However, theoretical ambiguity, regarding for instance the morphological diagnosability of early members of *Homo sapiens* and the significance of the label "multiregionalism" when applied to the African context, might hamper fruitful advances in the understanding of our historical past, failing to distinguish between what constitutes a genuine revision of previous narratives and what represents an integration. In what follows, we will go through some major assumptions of the recently developed pan-African model and some critical aspects, before sketching an integrative, evolutionary framing of the origins of *Homo sapiens*.

## 3. Pan-African view

### *3.1 Challenges and implications of Jebel Irhoud*

There is little doubt that recent discoveries and new dating efforts at Jebel Irhoud (Morocco) have played a major role in prompting the view that our origins may have involved the African continent at a broader scale, and over a longer period of time (Stringer 2016, Hublin et al. 2017, Richter et al. 2017). The site was discovered during mining activities in the '60s, and it has since then yielded many human specimens, notably an almost complete skull (Irhoud 1), an adult braincase (Irhoud 2) and an immature mandible (Irhoud 3). The interpretation of the fossils has long been highly controversial due to uncertainties in the geological age and their problematic mixture of archaic and derived (more *sapiens*-like) morphologies, swinging between different conclusions and implications (see Table 1 for an overview).

Hublin and colleagues (2017) – presenting a new human sample (cranial pieces Irhoud 10 and lower jawbone Irhoud 11), as well as stone tools and hunted animal remains, together with new thermoluminescence dating – suggested a new age for the Jebel Irhoud site at 315 ka (Richter et al. 2017), claiming that it documents "early stages of the *H. sapiens* clade in which key features of modern morphology were established" (Hublin et al. 2017: p. 289). This means that Jebel Irhoud belongs somewhere at the root of the monophyletic group that would eventually lead to *Homo sapiens*, but it is not yet itself *Homo sapiens*.

| **Interpretation of the fossil evidence** | **Dating** | **Key references** |
|---|---|---|
| African Neanderthal | ca. 40 ka | Ennouchi (1963) |
| No Neanderthal-like apomorphies | n/a | Santa Luca (1978) |
| Morphologically archaic but foreshadowing modern humans | 90-190 ka (ESR) | Grün, Stringer (1991) |
| North African *Homo sapiens* that has mixed with Neanderthals | n/a | Smith (1992) |
| Early *Homo sapiens* | ca. 160 ka (uranium-series and ESR) | Smith et al. (2007) |
| North African late surviving archaic population | n/a | Bruner, Pearson (2013) |
| Early stage of *Homo sapiens* clade | ca. 315 ka (thermoluminescence, ESR Irhoud 3) | Hublin et al. (2017)<br>Richter et al. (2017) |

**Table 1. Overview of various interpretations and chronology (when differing) of Jebel Irhoud fossils.** From their initial discovery in 1960, the Jebel Irhoud (Morocco) fossil assemblages have been subject to a variety of contrasting taxonomic interpretations, complicated by changing chronological inferences.

The findings are sometimes too hastily referred to as "the oldest *Homo sapiens* fossils" or "modern human fossils" not only by media coverage (Callaway 2017, Gibbons 2017), but also in scholarly publications (Bae et al. 2017, Hublin 2020). In fact, as also shown by Hublin and colleagues (2017) in their principal component analysis (PCA), in Jebel Irhoud specimens the braincase is elongated, with an angled occipital, so visibly not modern-like (see Fig. 2). On the other hand, the relatively short faces, with reduced brows, the mandibles (despite lacking a key modern feature, *i.e.*, the chin) and the dentition appear to be closer to modern variability (see also Bruner and Pearson 2013).

Significantly, the Irhoud fossils have been said to corroborate the interpretation of Florisbad material – craniofacial fragments and one tooth retrieved from South Africa – as a primitive *Homo sapiens* dated to ca. 260 ka. However, former taxonomic interpretations attributed the specimen to a "late archaic human" group (Grün et al. 1996), with some scholars distinctively classifying it as "*Homo helmei*", associated with Middle Stone Age (MSA) technology (Foley and Lahr 1997, McBrearty and Brooks 2000). Proponents of the pan-African view adduce the Florisbad skull as important material evidencing a widespread presence of early *Homo sapiens* from north to south of the African continent (Scerri et al. 2018). However, it is crucial for such claims to rest on reliable dates.

Grün and colleagues (1996) provided an age determination for the site of Florisbad, based on a molar that was assumed to belong to the same individual as the craniofacial fragments. However, the complex stratigraphy of the site and the lack of good records on the provenance of the fragments have led some to raise doubts on the contemporaneity of such remains and, consequently, on the actual presence of *Homo sapiens* in southern Africa at 260 ka (see *preprint* by Berger and Hawks 2020). Moreover, problems of taxonomic ambiguity remain. Previous reconstructions have already suggested that the Florisbad skull might belong to a more archaic species than *Homo* sapiens (Clarke 1985). Recently, also Bruner and Lombard (2020) have underlined that the mosaic pattern of derived and plesiomorphic traits (with the frontal squama considered within modern human variation, but with a Neanderthal-like anterior cranial fossa and *H. heidelbergensis*-like parietal lobe and vascular networks) is compatible with different phylogenetic scenarios.

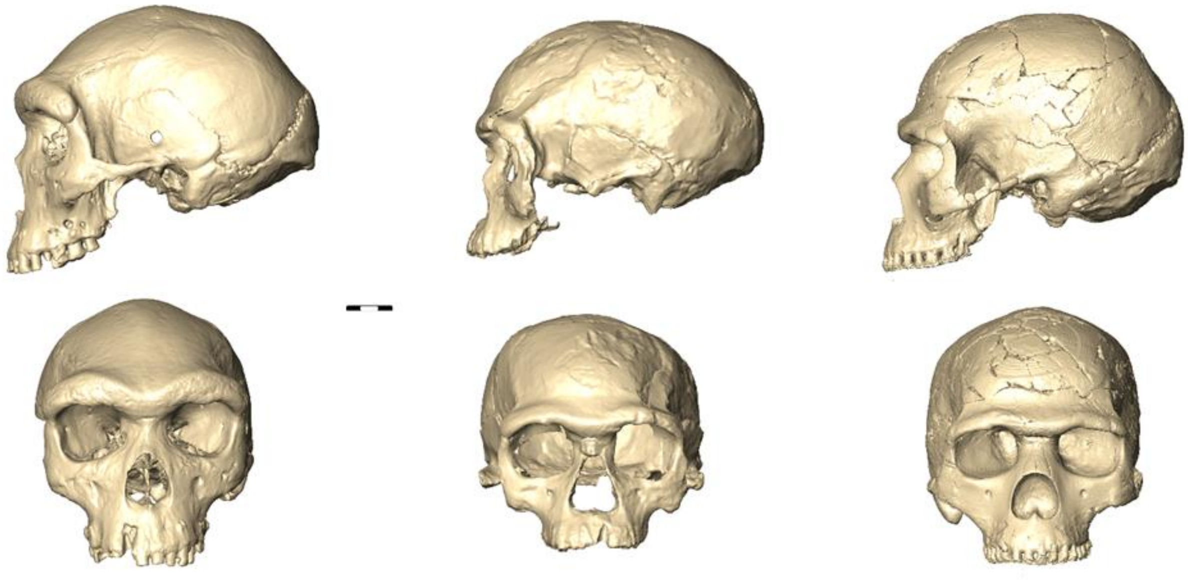

**Figure 2.** Differently "archaic": digital rendering of fossil specimens from **Broken Hill 1** (or Kabwe, ca. 299 ± 25, on the left side; Grün et al. 2020), **Jebel Irhoud 1** (ca. 315 ± 34 ka, in the middle; Hublin et al. 2017, Richter et al. 2017) and **Skhul 5** (ca. 100-130 ka, on the right side; Grün et al. 2005); although the facial shape of Irhoud shows some similarities with more recent specimens such as Skhul 5, its elongated cranial shape is clearly plesiomorphic, whereas the latter specimen exhibits a globular braincase and a high, vertical forehead, though combined with some reminiscence of "archaic" discrete traits (*e.g.*, the prominent brow ridges). Conversely, Broken Hill Is definitively more “archaic” in both architectural and discrete features.

Nonetheless, the Jebel Irhoud specimens offer important clues on different levels. First, they illustrate an evolutionary pattern that is gaining increasing attention in paleoanthropological research, namely the “mosaic evolution” of traits and hominin morphological instability (see Parravicini and Pievani 2019 for a review). In fact, especially at the beginning of the speciation process, key autapomorphies characterizing a new species do not appear as a fully assembled package within a single evolutionary trajectory: novelties can arise at separate intervals (*i.e.*, evolving at different rates and times) throughout hominin evolution, in an asynchronous fashion. Whether or not North Africa played some role in modern human origins (but see

Mounier and Lahr 2019), it seems clear that in late Middle Pleistocene populations a more modern-like face – more subject to different selective pressures – preceded the emergence of a globular braincase (Bruner et al. 2003, Bruner 2021).

A second implication confirmed by the Moroccan material is that, as already noted elsewhere (Manzi 2012, 2019, Grün et al. 2020), the origin problem is deeply rooted in the evolutionary mechanisms that shaped human variability during the Middle Pleistocene: a scenario characterized by marked phenetic diversity, that is still rather puzzling and, in some respects, little-known.

### *3.2 "African multiregionalism" and archaic metapopulations*

Scerri and colleagues (2018) have argued that the scenario according to which *Homo sapiens* evolved within a single population and/or region in Africa is challenged by a tangle of fossil, archaeological, genetic and paleo-environmental data, that are instead "consistent with the view that our species originated and diversified within strongly subdivided (i.e., structured) populations, probably living across Africa, that were connected by sporadic gene flow" (p. 582). In their recent review, Bergstrom and colleagues (2021) opened up for a more pluralistic perspective, in which the pan-African view is included within a range of possible models (of which only a complete replacement scenario from a single region seems to be rejected by current data). Here we refer to the pan-African scenario as detailed in full-length in dedicated publications (Scerri et al. 2018, 2019), drawing attention on interpretive compatibilities, terminological issues and evolutionary implications.

As regards the multiple lines of evidence called in support of pan-Africanism, we have seen above that caution in interpretation is merited on the fossil side: apart from uncertain dates, what we decide to keep in the "*Homo sapiens*" diagnosable box and what we leave outside is not a captious matter, but shapes significantly our understanding of the evolutionary trajectories at play. If there’s room for debate on the detailed suite of traits that should be considered diagnostic of our species and their degree or resolution, cranial globularity appears a less contentious point (Stringer 2016, Bruner et al. 2003, Lieberman et al. 2002, see also discussion in 4.2).

Pan-African proponents conceive *Homo sapiens* as an evolving lineage with deep African roots and consider fossils like Jebel Irhoud and Florisbad as part of the diversity shown by “early members of the *Homo sapiens* clade” (Scerri et al. 2018). They suggest that key-novelties like the derived shape of our cranium evolved *within* a lineage that was already to be considered *sapiens*-like, therefore drawing a distinction between the definition of *Homo sapiens* and what is to be considered an anatomically modern human specimen. This leaves then open the problem of morphological diagnosability along *Homo sapiens* lineage, if some key-criteria of anatomical modernity (notably, cranial globularity) need not to be met. Under more flexible diagnostic criteria, alternative taxonomic interpretations of early specimens, like J. Irhoud and Florisbad, in the absence of genomic data, cannot in fact be ruled out. This opens up the possibility, which we will explore in section 4, that a distinctive lineage emerged locally from a widespread archaic species with regional specializations and different combinations of derived and ancestral traits.

On the genetic side, under a pan-African scenario a deeper population divergence is expected. Schlebusch et al. (2017), based on Stone Age hunter-gatherers' genome sequences (from Ballito Bay, South Africa, ca. 2000 years old), estimated the deepest human population split time to 350 to 260 ka, separating the Khoe-San from all other extant humans. Divergence times inferred from genetic data are highly dependent upon mutation rate and generation time estimates, which are still a matter of controversy. More recently, analysis of whole genome ancient DNA from west-central Africa (extracted from children buried at Shum Laka site ca. 8 and 3 ka) slightly revised the previous threshold, indicating that at least four deep human lineages parted ways between 200 and 250 ka (Lipson et al. 2020). According to the authors, a “quadruple radiation” involved lineages leading to Khoe-San hunter-gatherers, Central African hunter-gatherers, East and West Africans, and a ‘ghost modern’ population. Different approaches might partly reflect different aspects of the divergence process, but the majority of human genetic ancestry seems to converge around 100 and 250 ka (Bergström et al. 2021).

These estimates could be compatible, in our view, with a complex and prolonged phase of "modernization" (ca. 350-250 ka) that preceded the coalescence of the full suite of derived traits, characteristic of our species. Such a phase might have followed in part the dynamics of a structured metapopulation described by Scerri and colleagues (2019): modern traits appeared through a mosaic pattern in a set of interlinked populations, whose connectivity and shifting isolation were shaped by paleoclimate dynamics and habitat opportunities.

In fact, we envisage this scenario for the emergence of our species as rooted in the story of the populations that were ancestral to *Homo sapiens* and *H. neanderthalensis* and that likely lived in Africa (Mounier and Lahr 2016, Manzi 2012, 2016). As we shall explain in the next section, in the case of a geographically widespread taxon it should be no wonder that populations start to evolve, at a local level, diversified combinations of ancestral and derived traits. This pattern is paralleled by regional diversification of early MSA toolkits (Scerri et al. 2018, McBrearty and Brooks 2000), that today however cannot be solely attributed to *Homo sapiens,* given the coexistence of multiple lineages in Middle Pleistocene Africa, that include *Homo heidelbergensis* (Grün et al. 2020) and *Homo naledi* (Berger et al. 2017).

The term “African multiregionalism”, that has been used to describe the pan-African view (Henn et al. 2018, Stringer 2016) is a further source of ambiguity in the debate – especially when associated with the expression “multiple origins” – due to an historical conflation of later versions of global multiregionalism with the candelabra model of racial anthropologist Carleton Coon (Wolpoff et al. 2000). The term “African multiregionalism” is rather a misnomer and should therefore be abandoned. In the African context, pan-African proponents value the role of gene flow among different contributing populations, which is neither compatible with the idea of a parallel mode of evolution nor with multiple independent origins. However, also the central principle of geographical continuity shared by multiregional models seems to be attenuated in favour of a more dynamic population history, which includes population fission, fusion, gene flow and extinction (Scerri et al 2019).

Yet, a metapopulation model so described seems overly flexible and therefore not easily falsifiable: depending on the degree of gene flow (which to date, in the absence of ancient DNA from earlier periods, remains speculative), it can accommodate both clean branching patterns and fully panmictic scenarios. In light of the above, the biological mechanisms that would promote a polycentric speciation over a vast and environmentally heterogeneous area like the African continent remain unclear. Scerri and colleagues (2018, p. 591) seem in fact to leave open the question of how many populations, geographical areas and environments actually played a role in the origins of *Homo sapiens.* However, how much gene flow should be hypothesised and over how long geographical distances? As for selection (if it is to play a role), what kind of strong and persistent selective pressures, acting over a vast and heterogeneous geographic scale would have led different populations to evolve the diagnostic traits of our species? Even more importantly, what kind of biophysical and paleoclimate setting would have allowed a pan-African-like process to unfold?

## 4. An evolutionary and biogeographical framing for the origin problem

The available evidence and conceptual nodes animating the current debate suggest that the emergence of *Homo sapiens* should be understood as a multi-phase process. Within this framework, we argue that from the initial conditions represented by an ancestral metapopulation (i.e., the putative LCA), characterized by demographic complexity, morphological variability and shifting structure, a more derived form – *i.e.*, a "crown node" (Hennig 1969, Budd and Mann 2020) – likely emerged locally. This would have later expanded across Africa, interbreeding with populations of the LCA, as well as in Eurasia, where there is evidence of gene flow among *Homo sapiens* and its sister taxa (Green et al. 2010, Reich et al. 2010).

Africa is indeed a vast continent (30.3 million km$^2$), covering 20% of Earth's land area, and the conclusion that *Homo sapiens* evolved throughout Africa is not very informative. To think about human origins in relation to contributing geographical locales means interrogating the factors that led to the formation of regional population structure and, in the case of a major contributing area, gaining clues on the circumstances of the occurrence of a new phenotype. Since gene flow happens among contiguous populations and a fully panmictic scenario is not very plausible over such wide areas, it is unlikely that the source populations have all contributed (or have contributed equally) to the emergence of *Homo sapiens*.

Given the initial starting conditions – that of a structured original population spread across different regions of the continent – two are the possible outcomes (Fig. 3):

a) derived *Homo sapiens* evolves in different geographical locales, almost within the same temporal window, with the contribution of diverse populations (pan-Africanism);

b) the ancestral metapopulation, characterised by a mosaic of archaic and derived traits, yields an allopatric and punctuated emergence of a morphologically distinctive group, displaying for the first time a globular braincase. Through subsequent expansions and admixture with lineages of the parental species, other evolutionary novelties are incorporated and stabilized within that expanding deme.

We favour the latter alternative, which should be referred to as an *"extended" single African origin*, in order to distinguish it from older oversimplified narratives.

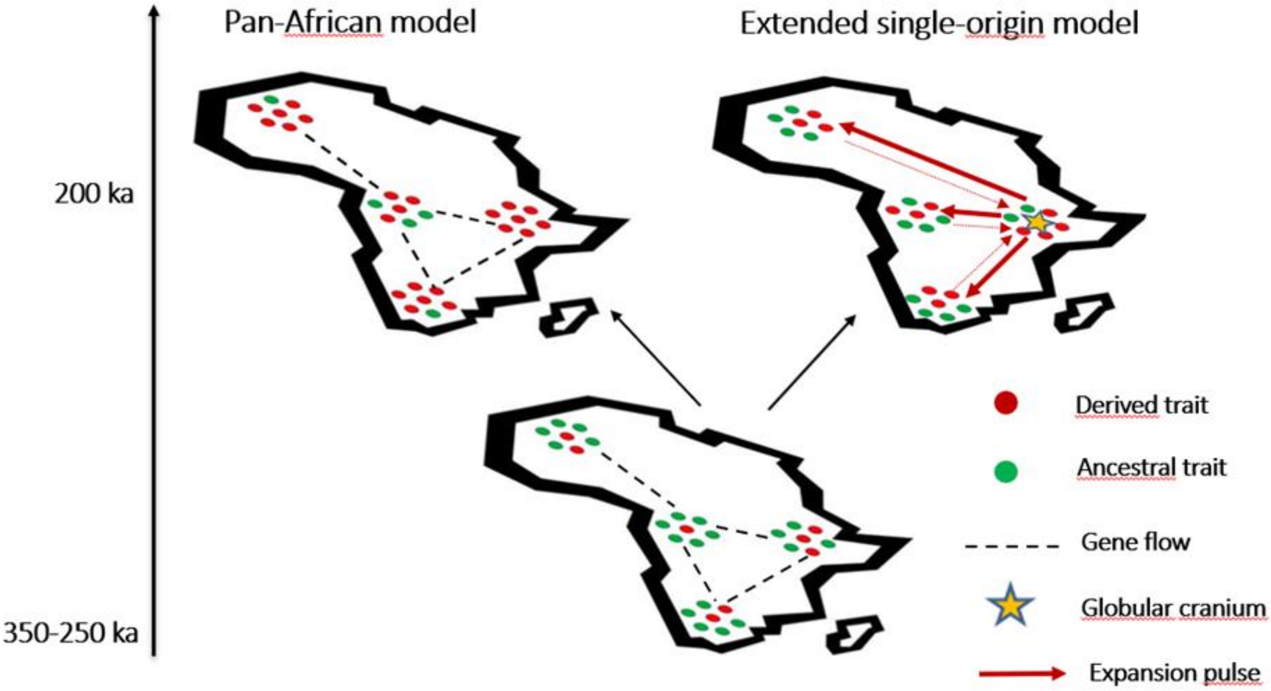

**Figure 3. Scenarios of modern human origins in Africa in the past 350.000 thousand years.**

On the basis of the currently available data, a Pan-African (left) *vs.* an "extended" single origin (right) of *Homo sapiens* are two possible outcomes of a structured pre-modern metapopulation (LCA) of the Middle Pleistocene, connected by gene flow (dashed lines) and characterized by a combination of ancestral (green dots) and more derived traits (red dots).

We note also that these scenarios resonate well with the models recently proposed in a review by Bergström and colleagues (2021, fig. 2a in their paper), namely the model of the "long-standing pan-African connectivity" and that of the "expansion pulses". Their review fruitfully distinguishes three major phases in recent human evolution: i) the separation of modern human ancestors from archaic human groups (from 1 Ma up to 300 ka); ii) the African origin of modern human diversity (300-60 ka); iii) the worldwide expansions with modern humans and their contacts with Neanderthals and Denisovans (40-60 ka). Interestingly, Bergström and colleagues claim that both the pan-African and the expansion pulse hypothesis are today difficult to test against genomic evidence, which makes a discussion on the evolutionary reasons to prefer one over the other particularly relevant, in order to provide a biological framing for these scenarios. In what follows, we will approach the debate in terms of a speciation process arising from the hominin variability in Africa during the late Middle Pleistocene and will consider the role of climatic context in shaping biogeography, selective conditions, and connectivity among different demes. To do so, it is necessary to spell out what is meant by "speciation" and "species" in this context, and the significance of cranial globularity as a modern morphological trait.

### *4.1 Species and speciation*

Evolutionary theory indicates (following Mayr 1942, 1963) that the bulk of speciation processes occur where populations are geographically isolated (*i.e.*, allopatric condition) in relatively small areas of the parental species range (Coyne and Orr 2004, Gould 2002). A recent and comprehensive review on speciation modes conducted across major taxonomic groups confirms allopatric speciation as the likely dominant mode across vertebrates (Hernández-Hernández et al 2021).

Punctuated patterns emerge as the expected scaling of ordinary allopatric speciation into geological time, thus bearing implications for the fossil record (Eldredge and Gould 1972, Gould and Eldredge 1977). Departure from such a "null-model" of speciation (in terms of its relative frequency; Allmon 2016), as implied in the pan-African view, would require a clear evolutionary framing that has to explain why *Homo sapiens* should constitute an exception. If an anagenetic mode of speciation (phyletic change) is implied – although not explicitly framed with such terminology – the ecological and biogeographical conditions allowing such a process to unfold on a continental scale should be addressed. We also note that population differentiation represents a first step in the process of allopatric speciation and that a new species should arise more quickly from a structured metapopulation in an isolated (or semi-isolated) context than within a wide-range genetic cohesion maintained through gene flow.

By underlying the importance of a geographic view on the speciation process, we do not intend to imply that species should be defined by strict reproductive isolation (Mayr 1942). We recognize in fact the input of gene flow at all phases in *Homo sapiens*' speciation process (see below and Fig. 5). More generally, in the vast and complex literature on the "species problem" (Hey 2001, 2006), there has grown a common thread of argument claiming that many of the available species concepts share the underlying idea of species as evolutionary groups having a common evolutionary history (or as separately evolving metapopulation lineages, *e.g.* de Queiroz 2007). It is also clear that various properties on which delimitation is based (including reproductive isolation) do not appear simultaneously, but accumulate and become increasingly marked over time.

Therefore, we believe it is plausible that during the speciation of *Homo sapiens* some crucial phenotypic autapomorphies, like a globular neurocranium, have emerged locally, indicating that a separately evolving lineage was already underway. These would have subsequently started to spread, thus progressively enriching and stabilizing the suite of modern morphological traits. As for *complete* reproductive isolation, being a function of divergence time, it should not be expected among closely related lineages that have separated in recent evolutionary time.

On the other hand, if pan-Africanism better describes our evolutionary history, we should observe in the fossil record highly derived forms, with features of cranial globularity (such as those characterizing the Eastern African record), in geographically dispersed regions and at a broadly penecontemporaneous time. These predictions can be tested against the available evidence.

### *4.2 Globularization*

There is an extensive consensus among researchers that, when cranial anatomy is considered, the morphology of *Homo sapiens* is characterized by a significant facial retraction (with a forward protrusion of the chin) and by a noticeable globular expansion of the cranial vault (e.g., Lieberman et al. 2002, Bruner et al. 2003, Stringer 2016, Gunz et al. 2012, 2019). The extant human populations largely share a globular neurocranium, as amply demonstrated by several studies that have approached the dichotomic variability observed in comparing the fossil record and more recent human samples (*e.g.*, Mounier & Mirazón Lahr 2019). This, in turn, points out a distinction within the genus *Homo* between "archaic" (*i.e.*, characterized by an antero-posteriorly elongated cranial vault) and "modern" humans with a rather globular braincase.

As in the example reported in Fig. 4A, when a principal component analysis is performed on geometric morphometric data of the human cranium, samples representing the range of modern variability (including fossil specimens of the Late Pleistocene) are clearly distinct from representatives of both archaic and early *Homo*. The analysis explains this distinction in terms of different cranial architectures: elongated (archaic) vs. globular (modern) shapes. Therefore, despite the expression of a globular braincase is variable across recent human populations and although modern morphology had a basis in some Eurocentric typological thinking of the past, globularity itself appears a species-specific trait of *Homo sapiens* also in recent studies that include worldwide, extant population samples (Bruner et al. 2003; Mounier & Mirazon Lahr 2019).

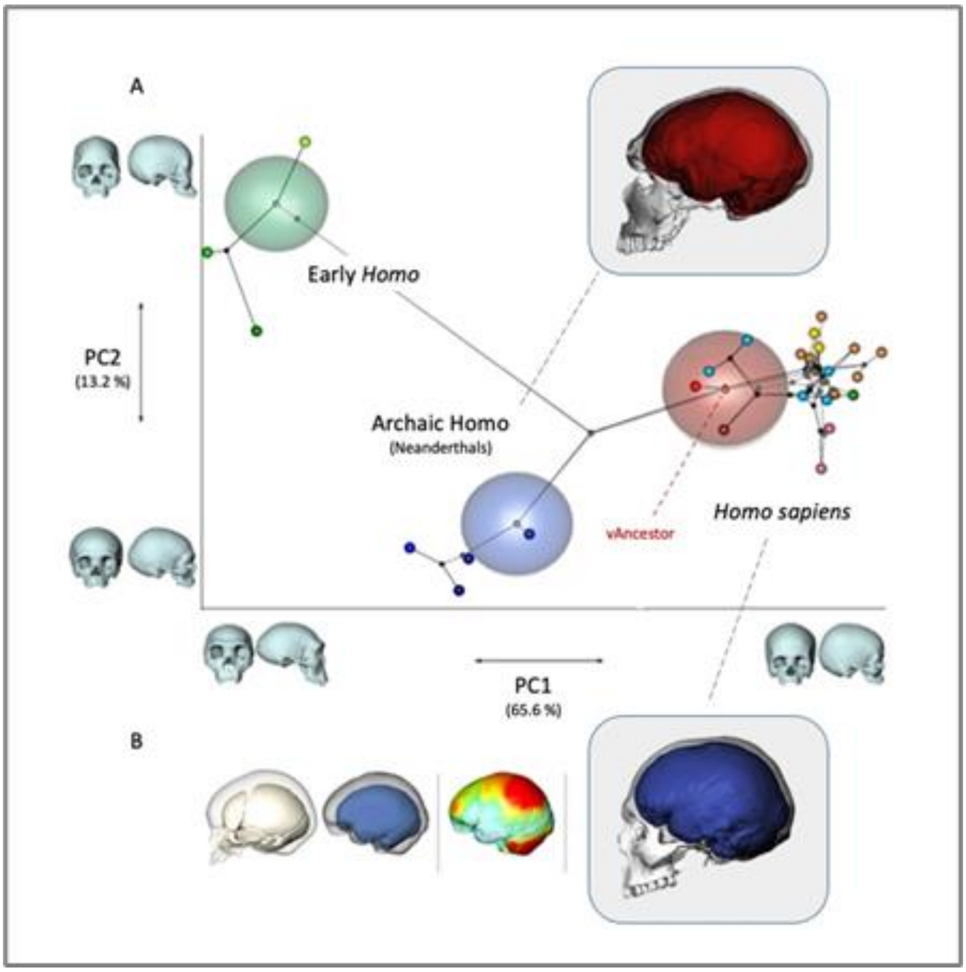

**Figure 4. Projection of three *Homo* groups into the morphospace and modern human globularization.** The modern cranial architecture (i.e., the cranial shape of *Homo sapiens*) is clearly distinguishable from more archaic morphologies, as it is demonstrated by a PCA based on geometric morphometric data (A); moreover, this is the result of a peculiar developmental process leading to its globular appearance (B). This picture combines Fig. 2 in Mounier & Mirazón Lahr (2019) and Figs. 1 and 2 in Gunz et al. (2012): see references for detailed legends.

It has been also demonstrated that the morphological changes underlying the globularity of our neurocranium occur early in ontogeny (see Fig. 4B), particularly during the first year of life (Neubauer et al. 2010, Gunz et al. 2012). As concerns the endocast (brain and meningeal membranes), changes involve a "neomorphic hypertrophy of the parietal volumes, leading to a dorsal growth and ventral flexion (convolution) and consequent globularity of the whole structure" (Bruner 2004, p. 279). Moreover, it has been suggested that endocranial globularity might reflect evolutionary changes in early brain development (Gunz et al. 2010). According to some cognitive psychology assessments,  the development of a globular brain could pertain to the biological foundations of the language faculty in *Homo sapiens* (*e.g.*, Boeckx & Benítez-Burraco 2014; see also Di Vincenzo & Manzi 2013).

In our view, it is reasonable to conclude that: i) cranial globularity is a crucial species-specific trait of the modern human species; ii) this complex feature is related to significant changes in the developmental program and its underlying genetic regulation – thus, it should be viewed from an evo-devo perspective (Hublin et al. 2015; Neubauer and Gunz 2018); iii) its settlement was probably the result of an episodic event, given that all the other encephalization trajectories that developed in the last two million years across the radiation of the genus *Homo* (with the single peculiar exception of *Homo floresiensis*), led to a different – *i.e.*, elongated – morphology of both the cranial vault and its endocranial content. We believe that these conclusions should be accommodated in any speculation about the origin of *Homo sapiens*.

### *4.3. Extended single-origin: a renewed scenario*

The remains that should be considered in an extended perspective of the chronology and geography of the emergence of modern humans are those characterizing the phenetic diversity that is recorded across Africa in the late Middle Pleistocene. A morphological pattern characterizes samples after ca. 600 ka (with the period bracketed between 900 and 600 ka being marked by a poor fossil record; but see Profico et al. 2016; Zanolli and Mazurier 2013), including the retention of ancestral traits for the genus *Homo*, like an elongated cranial vault, combined with more derived ones, such as an increased cranial capacity, a peculiar form of the supraorbital torus and a less flattened midsagittal profile (Mounier et al. 2011).

These derived human varieties appear distributed on a vast geographical range, spanning from Africa to Eurasia (see Stringer 2002, Manzi 2012 and Berger et al. 2017 for reviews and datings), jointly with the persistence of morphologies that are more reminiscent of earlier hominins, both in Africa (i.e., *Homo naledi*) as well as in the Far East (e.g., late *Homo erectus* as well as *Homo floresiensis,* Brown et al. 2004). In Africa, examples come from Ethiopia (Bodo, 600 ka), Kenya (Eliye Springs, ca. 300-200 ka and Guomde, ca. 270-300 ka), Tanzania (Ndutu, ca. 400 ka; Ngaloba, ca. 300-200 ka), Zambia (Broken Hill or Kabwe, recently redated to ca. 299 ka; Grün et al. 2020), and South Africa (Elandsfontein, ca. 600-1000 ka), in addition to specimens we already discussed such as Florisbad and Jebel Irhoud. This rather polymorphic record was usually referred to in the past as "archaic *Homo sapiens*" and more recently it has been viewed as representing one or more species, such as *Homo heidelbergensis* and/or *Homo rhodesiensis* and/or *Homo helmei* (Foley and Lahr 1997, McBrearty and Brooks 2000).

These variable morphologies of the late Middle Pleistocene provide the context to think about the basal population of anatomically modern humans, particularly in a period in which localized populations were strongly subject to both selective pressures and genetic drift. Looking at the paleoclimate setting, there is evidence of a major inflection point after 430 ka (the Mid-Brunhes Event, MBE, close to the boundary between MIS 12-11), after which an increased climate variability is observed, with the development of colder glacial periods and warmer interglacial phases (deMenocal 2004, Jouzel et al. 2007). Continental pollen record from Lake Magadi provides strong support for a significant climatic transition at MBE, marking a major shift from wetter conditions to greater aridity after 430 ka (Owen et al. 2018). In particular, the period between 350 and 50 ka is the longest episode of eccentricity-modulated high-amplitude insolation variability in the Middle to Late Pleistocene (Owen et al. 2018). In the South Kenya Rift this period was marked by significant environmental and hominin change, that has been interpreted as providing evidential support for hypotheses like variability selection, according to which adaptive evolutionary change most likely takes place within episodes of increased environmental variability (Potts 2013). In this regard, Potts and colleagues (2018) have recently hypothesized that the emergence of the MSA technology and the complete replacement of the Acheulean in southern Kenya around 320 ka represents an evolutionary, behavioural response to foraging unpredictability and changing resource landscapes (as a result of prolonged wet-dry climate oscillations), also responsible for a faunal turnover.

Change in climate, fluctuation in precipitations and environmental instability that were asynchronous between geographic regions (Blome et al. 2012) may have well played a significant role in shaping population structure and spatial variation in morphology during late Middle Pleistocene. Therefore, as a result of phases of isolation due to challenging environments, archaic traits might have been retained by some populations, such as in the case of specimens like Kabwe 1 (or Broken Hill cranium) or even entire species such as *Homo naledi*.

Geographic restructuring due to changing climatic conditions might have contributed to population separation and isolation as well as to creating corridors and opportunities for migration and gene flow (that might have involved also distantly related groups; Hammer et al. 2011, Durvasula and Sankararaman 2020). We know in fact that during dry interpluvial periods, the decrease in precipitation and $CO_2$ favoured the expansion of savannah coverage, with a northward shift of southern hemisphere grasslands and an increase in West African savannahs at the expense of lowland forests. Conversely, during moist pluvials, expanding tropical forests replaced grasslands (Dupont 2011, Cowling et al. 2008). This recurrent environmental reshuffling, as well as the role of refugia as important catalysts of population contraction and evolutionary change during glacial cycles (Stewart and Stringer 2012) have conditioned population connectivity and divergence. Crucially, major changes to climate and ecosystems might have well prompted significant macroevolutionary changes, like speciation events. The biogeography of non-human taxa offers other important clues, confirming this scenario. Studies on ungulates, for example, have identified in East Africa a major zone of endemism, where environmental instability facilitated spatial and temporal refugia, and a “suture zone”, *i.e.* an area where lineages that have diverged in allopatry come into secondary contact (Lorenzen et al. 2012). Notably, also Vrba’s research on African mammalian fauna concluded that climate change initiated a substantial species turnover, with increased aridity and seasonality being a major stimulus. There are numerous examples of anatomical and behavioural changes in mammals that roughly coincide with the appearance of hominin novelties and show similar patterns (Vrba 1992, 2015).

It is often overlooked that evolutionary change involves different levels of the evolutionary and ecological hierarchies, from genes to ecosystems (Eldredge 2008, Parravicini and Pievani 2016). Microevolutionary explanations of changes occurring below the species level and in populations (*i.e.* changes in gene frequencies, the action of selective pressures and genetic drift) are biologically meaningful if seen under the light of macroevolutionary patterns shaped by ecological and climatic processes, as emphasised among others by Vrba (2015).

What can discriminate between the two abovementioned evolutionary outcomes – pan-Africanism vs. a major contributing region in our evolution (*i.e.*, an extended single African origin) – is therefore the role played by the paleo-biogeographical setting, including: presence of geographic barriers; distance among populations; disruptiveness of climatic events that have shaped the degree of vicariance among LCA populations.

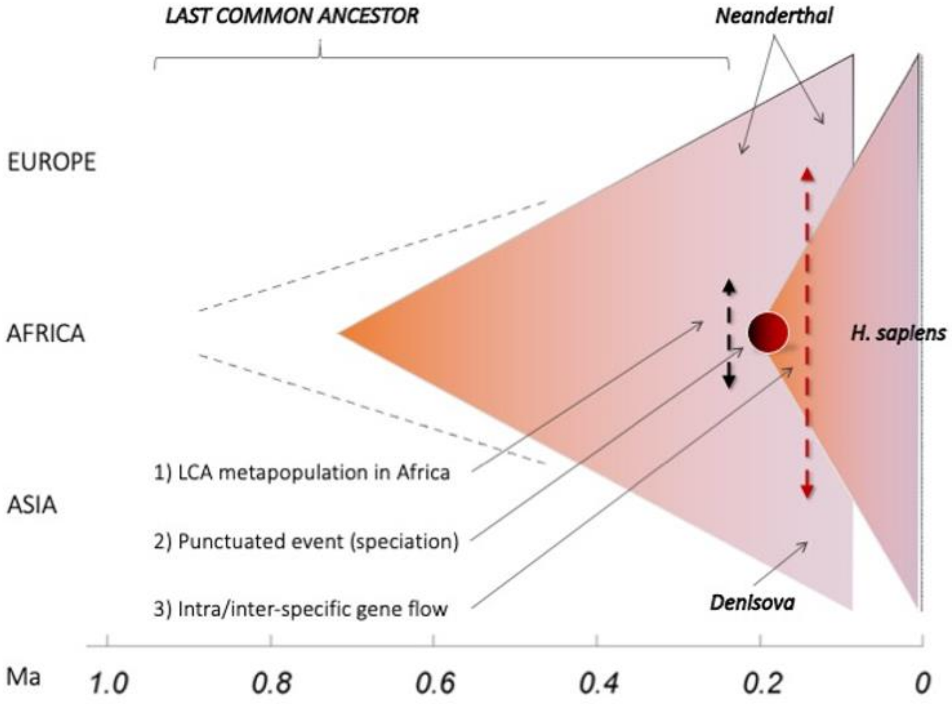

**Figure 5. A three-step process for the evolution of *Homo sapiens***: (1) mosaic combination of traits among demes of the LCA metapopulation in Africa; (2) allopatric and punctuated emergence of cranial globularity in an isolated population (indicated by the dark red sphere); (3) expansion of the deme carrying a globular neurocranium across Africa and towards Eurasia. Dashed lines indicate gene flow among populations of the same and/or different species both in Africa (black) as well as within and outside Africa (red).

Our model of an extended single African origin suggests that it is possible to provide a synthetic framework coherent with evolutionary knowledge and the role of environmental and climatic constraints. We thus suggest a three-phase process (Fig. 5). It is likely that after a phase of mosaic evolution among late LCA populations (phase 1), in a context of environmental changes a set of derived traits concerning face and dentition coalesced in an isolated population that displayed for the first time the crucial morphological novelty of a globular neurocranium (phase 2), which appears in the Eastern African fossil record as a punctuated evolutionary change ("crown node"). These traits would have subsequently stabilized and enriched the suite of modern morphological traits through expansion pulses and gene exchanges with other populations of the LCA within the continent and, later, with closely related species that evolved outside Africa (phase 3).

Summing up, the period of dramatic climatic instability that is close to about 200 ka (MIS 6) may plausibly correspond in Africa to the condition in which an isolated population experienced the crystallization of long-term evolutionary processes, culminating in our fully derived anatomical features, whose uncontroversial earliest fossil evidence has been so far encountered in the Ethiopian sites just after 200 ka.

## 5. Concluding remarks

In this paper, we critically reviewed evidence regarding two alternative scenarios for the origin (*i.e.*, the speciation) of *Homo sapiens*, within the more general paradigm of Recent African Origin or RAO: the single-origin hypothesis and the pan-African model, which assumes a polycentric appearance for the suite of modern human autapomorphies.

We argued that the former hypothesis represents a sort of "evolutionary ordinariness", being more parsimonious with respect to a continent-wide speciation for *Homo sapiens* and more compatible with the present background knowledge in evolutionary biology, as it would most likely be predicted for other vertebrate or mammalian species. By contrast, the latter scenario appears more appropriate for a microevolutionary process of diversification, leading to sub-specific taxonomic ranks. When viewed from a macroevolutionary perspective, it might also describe the evolutionary history of the entire group – *i.e.*, a "pan group" – from which our species ultimately originated and therefore includes also the putatively ancestral, geographically widespread and phenetically diversified (as well as taxonomically controversial, cfr. Roksandic et al. 2021) *Homo heidelbergensis*, as well as the diverging Neanderthal and Denisovan lineages, viewed as part of the crown group that includes *Homo sapiens*.

We argue that this scenario is nonetheless compatible with a major event of speciation for the origin of *Homo sapiens*, which was allopatric with respect to the Neanderthals and Denisovans; at the same time, it was more probably punctuated (within the wide African scenario), in view of the crucial appearance of a globular braincase. It is not irrelevant that such a crucial novelty for the identity of *Homo sapiens* is exhibited for the first time in the East-African fossil record (Omo-Kibish 1, Herto). Although subsequent modern populations share a suite of morphological traits – *i.e.*, a more gracile face or a modern-like dentition – with some other African samples of the late Middle Pleistocene (*e.g.*, Jebel Irhoud, Florisbad) is not sufficient to envisage these samples as part of the same crown node. Instead, they may better represent the occurrence of a stem group emerging from the same basal node. What is informative in our view is that such novelties coalesce geographically and are accompanied by the key autapomorphies of the neurocranium, thus suggesting an important reshuffling of the ontogenetic process. Actually, as pointed out by late palaeontologist Stephen J. Gould, the persistence of alleged ancestral populations after a cladogenetic event should not represent a problem from an evolutionary point of view, as it has been prominently featured in paleobiological literature (Gould 2002).

## Acknowledgements

We are particularly grateful to Fabio Di Vincenzo, as well as to the Editor of Evolutionary Anthropology Jason Kamilar, Marta Mirazón-Lahr and two other anonymous reviewers, who provided suggestions that have been of great help for improving the original manuscript. This research was supported by Fondazione Cassa di Risparmio di Padova e Rovigo, CaRiPaRo (A.M.).

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# 3.

# The transition to “Behavioural Modernity”

## Behavioural Modernity, Investigative Disintegration & Rubicon Expectation

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## Abstract

‘Behavioural modernity’ isn’t what it used to be. Once conceived as an integrated package of traits demarcated by a clear archaeological signal in a specific time and place, it is now disparate, archaeologically equivocal, and temporally and spatially spread. In this paper we trace behavioural modernity’s empirical and theoretical developments over the last three decades, as surprising discoveries in the material record, as well the reappraisal of old evidence, drove increasingly sophisticated demographic, social and cultural models of behavioural modernity. We argue, however, that some approaches to identifying and categorizing modernity have not kept up with this new picture. This is due to what we term ‘Rubicon expectations’: classificatory and interpretive practices which look for or assume clear demarcations in behavioural and cultural processes.

We develop a philosophical account of ‘investigative disintegration’ to capture how our understanding of behavioural modernity has changed, and how Rubicon-based practices have become inadequate. Disintegration, in the form we analyse, occurs when scientists’ conception of a phenomenon shifts sufficiently to reshape an investigation’s epistemic structure. For behavioural modernity, the explanatory weight which once lay on identifying ‘switch-points’ in the innate suite of hominin cognitive capacities, lies now in understanding the social and demographic environments that were capable of sustaining and nourishing more complex material cultures. Finally, we argue that the phenomenon itself has not disintegrated to the point that we are left with no interesting *explanandum*: for all its mosaic, disparate nature, there are still good reasons for behavioural modernity to retain its central place in investigation of our species’ origins.

## Keywords

Archaeology; Behavioural modernity; Cumulative cultural evolution; *Homo sapiens*; Investigative disintegration; Rubicon expectation.

## 1. Introduction

Generalist accounts of science’s structure and progress have failed: science is a far too heterogeneous, contingent and human beast for universally applied, abstract schema to gain traction. In light of this, philosophers are developing local, context-sensitive and pragmatic models of science. Reduction is replaced with mechanistic understanding (Machamer, Darden & Craver 2000), unity with local integration, disunity with a patchwork of independent and interdependent representations, epistemic goods and tools (Wylie 1999, Brigandt 2010, Potochnik 2010, Mitchell 2003). Much work in this vein has attended to the formation and stability of research; how local integration and independence between evidence, theories and institutions structure science and its epistemic standing (Chang 2012, Ankeny & Leonelli 2016). However, progress in scientific investigation isn't solely attained via *integration*, that is, aligning new data into stable theoretical horizons, research strategies and agendas. New data and new re-readings of available data may also disrupt fundamental research questions, approaches and concepts. In this paper we examine such disruption: investigative *dis*integration. How new, unexpected results reshape our conceptions of target phenomena, thus reshaping epistemic landscapes.

We'll examine disintegration through a close look at developments in the study of our species' behavioural origins. 'Behavioural modernity' traditionally indicates distinctively human behavioural and cultural expressions. The notion was initially introduced to mark the perceived time-lag between the apparent arisal of *H. sapiens* —*anatomical* modernity—now set at ca. 300-200kya (McDougall et al. 2005, Hublin et al. 2017, Schlebusch et al. 2017, Lipson et al. 2020), and the stabilization of the archaeological assemblage associated with characteristic human behavioural and cognitive capacities, such as sophisticated sociality or symbolic expression, after ca. 100-50 kya (Renfrew 1996, 2009, Henshilwood and Marean 2003). The temporal mismatch was thought by archaeologist Colin Renfrew to pose a genuine explanatory puzzle – the so-called "sapient paradox": why did it take more than 100.000 years for the modern body to meet the modern mind?

Over twenty years, a richer set of archaeological and paleontological specimens, as well as genomic data from Africa and globally, provided richer contextual information about population and species distribution, migration and interaction, and more sophisticated accounts of the factors underlying material complexity (see Galway-Witham et al. 2019 for a review). As we'll describe in section 2, what counts as a relevant archaeological signal in this context has been progressively rethought and the evolutionary models explaining such signals have been complexified, thus significantly reshaping our conception of behavioural modernity.

Today, the nonlinear and divergent ways in which traits of behavioural modernity appeared in various regional contexts are ever-more emphasized features of the archaeological record. Recent research has increasingly moved away from saltationist and hardwired causal approaches, making older classificatory and interpretive strategies no longer on par with current epistemic standards, yet some of these are retained. In section 3 we highlight one example of this – *Rubicon expectation* – where archaeological investigation and categorization are expected to provision a kind of 'switch-point' marking where and when the phenomenon arose. For behavioural modernity, this involves identifying discrete and unambiguous cognitive or behavioural boundaries that should divide early and late anatomically modern humans (AMHs)[1], or biologically distinct hominin species.

To capture these crucial features in the evolution of the research surrounding behavioural modernity, in section 4 we will develop an account of 'investigative disintegration'. Investigations disintegrate when a once-clear phenomenon becomes complexified such that the epistemic structure of the investigation transforms. Disintegration, we'll show, doesn't simply involve changes to empirical and theoretical regimes but shifts in *explanatory weight*. Previously, the explanatory weight on accounts of behavioural modernity fell on explaining when and how distinctive cognitive and behavioural clusters of traits arose. In the new context the explanatory weight falls on the conditions by which such traits became sufficiently stabilized at a regional scale for cumulative cultural evolution. We'll argue that recent discoveries and new interpretive perspectives have changed the explanatory game such that

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[1] Although the usage of the term "anatomically modern humans" may vary in scope, it was introduced to distinguish hominin fossils that fall within the range of today's human skeletal variation from otherwise anatomically "archaic" forms.

‘Rubicon’-style explanations and approaches to categorization are not adequate for the current research agenda, and thus cannot carry the explanatory weight required for understanding the phenomenon.  We’ll argue that in light of investigative disintegration the significance of archaeological discoveries regarding modernity should shift, but that despite all this, the concept of ‘behavioural modernity’ should be retained.

Our paper, then, is intended both to provide a philosophical analysis of ‘investigative disintegration’, which we suspect is a not-infrequent scientific phenomenon, and to apply our analysis to the evolving research agenda targeting behavioural modernity. We’ll do this in two major steps. The first, sections 2 and 3, will summarize and critique research on behavioural modernity. The second, comprising sections 4 and 5, will shift to more abstract philosophical analysis, analysing investigative disintegration and bringing it to bear on behavioural modernity.

## 2. Behavioural Modernity in hindsight

How ‘behavioural modernity’ is understood, as well as the proposed mechanisms underlying its emergence, have been radically transformed (d’Errico and Stringer 2011, Davies 2019). In this section, we’ll discuss how the relationship between the archaeological record and the phenomenon at hand has shifted as new data has come online, before tracing the new explanatory models that have been produced in light of this.

### *2.1 Signals of Modernity*

From an archaeological perspective, ‘behavioural modernity’ can be understood as a phenomenon inferred from the record based on a constellation of material proxies taken to be revelatory of complex cognitive, technical and social lives. Debate, then, often turns on the appearance and distribution of such proxies (Henshilwood and Marean 2003). These traditionally took the form of 'trait-lists': an inventory of discrete detectable material signatures taken to provide universal indicators of modern behaviour. Common examples are new lithic technologies (blades and microblades), the appearance of composite tools; worked bone, antler and ivory; long distance exchange of raw materials; seasonal mobility and exploitation of resources; elaborate and varied art forms such as engravings, sculptures and cave paintings; musical instruments; widespread use of personal ornaments; manipulation of symbol and notation systems (cfr. McBrearty and Brooks 2000, Henshilwood and Marean 2003, Ames et al 2013).

Such trait-lists were initially based on Upper Palaeolithic European sites (henceforth UP; Mellars and Stringer 1989, Gamble 1994). Through the noughties lists more reflective of the African Middle Stone Age (MSA) were developed in an attempt to correct this Eurocentric bias (McBrearty and Brooks 2000, Deacon 2001). Critically, signatures were no longer treated as a package deal or a 'syndrome', instead they were taken to reflect scattered origins in space and time. Lately, research has targeted particular aspects of material culture thought to provide clear signals of behavioural modernity: what we call archaeological "golden spikes". These focus especially on symbolic expression tied to, for instance, pigment processing (e.g., ochre) or bead production (Wadley 2001, Henshilwood and Marean 2003, Tattersall 2008, Marean 2015).

It now seems like an obvious mistake to use the European UP record (ca. 40 to 10kya) as an empirical yardstick to establish contrasts between late and early modern *Homo sapiens* in Africa (Deacon 2001; D'Errico 2003; Henshilwood and Marean 2003; Shea 2011). However, some have argued that recognising the limitations and European origin of such working definitions has neither led to complete abandonment nor to replacement with substantially different approaches (Barham and Mitchell 2008). Employing the record of any single region as a standard for judging global patterns in human evolution risks conflating regional dynamics and universal trends (especially if fieldwork has been historically prioritized in that region, Gamble 1999, Shea 2011). To see this, let's trace some influential developments in how modernity has been detected in the archaeological record.

Against Eurocentrism, McBrearty and Brooks (2000) developed a trait list aimed at better reflecting the depth and complexity of the African archaeological record, thus showing that many purported European innovations had African precursors. They proposed four sets of traits characterizing modern behaviour: abstract thinking; planning depth; behavioural, technological and economic innovativeness and—notably—symbolic behaviour. These were linked with numerous archaeological signatures which were taken to demonstrate their acquisition. As we'll see in 2.2, the overall model behind the appearance of such traits differs substantially from those developed based on the UP European package. However, the list, as D'Errico (2003) rightly noted, lacked cross-cultural comparative analysis of various human societies and was still derived from local material culture (African MSA and, to a lesser extent, the UP). This, he argued, provides poor heuristics for testing modern characteristics of populations living in different environments which might have followed different evolutionary trajectories.

Henshilwood and Marean (2003) identified four major flaws in defining behavioural modernity through trait-lists (or, as Wadley 2001 ironically called them, "shopping lists"): empirical derivation, ambiguity, lack of theoretical grounding and taphonomic bias[2]. Although these objections first applied to European-derived traits, they are plausibly applicable to any attempt to approach modern behaviour through trait-lists developed from particular sites and particular time periods as opposed to world-wide anthropological and ethnographic data (see also Wynn et al 2016). So, deriving markers from geographically localized archaeological records (be they

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[2] Taphonomic bias refers here to the differential preservation in the archaeological record of the traits used to diagnose behavioural modernity. This can likely lead to false negative findings about modern behaviour in regions where the potential for preservation is generally low.

African MSA or European UP) makes behavioural modernity unambiguously recognizable only in the records on which the list was based (D'Errico and Banks 2013). Further, proxies taken to signal newly evolved capacities may instead be reactions to resource intensification or population pressure (hence, they are ambiguous because other processes can be invoked to explain their appearance in the record). Moreover, the inclusion of some traits in the lists seems to lack proper theoretical justification: for example, seasonal mobility, besides varying widely among living humans, is known to be practiced by some non-human species as well (Wadley 2001). Finally, as with many archaeological investigations, taphonomic biases are a constant worry, especially in equatorial contexts where biotic preservation (e.g. bone or antler tools) is unlikely.

Having critiqued trait-lists as being inherently flawed, Henshilwood and Marean conclude that a better approach would be to instead focus on one particular proxy that gathers consensus for being a crucial modern human feature: symbolic expression and its material signatures. Frequently cited are data signalling symbolic capacities from South African sites, such as mineral pigment modification (ochre) and perforated shells found at Blombos Cave (100-70 kya), later reinforced by new finds and revised dates at other sites (see Wadley 2015 for an updated review). This all led to a growing focus on a "golden spike" for modernity: the entry into the record of materials thought to unambiguously signal symbolism. These, as we'll show, are in fact equally susceptible to the flaws identified for trait-lists. In section 4 we'll argue that both trait-lists and 'golden-spikes' are problematic when used as Rubicons, in light of investigative disintegration.

Another thread running alongside debates about proxies asks whether behavioural modernity can (or should) identify a unique set of behaviours characterizing AMHs and not other hominin species. Where previously behavioural modernity was meant to distinguish our species from Neanderthal proxies, as Zilhao provocatively noted these often ended up "defining some modern humans as behaviourally Neandertal and some Neandertal groups as behaviourally modern" (2006). As archaeological signals of behavioural modernity became increasingly diffuse, identifying the phenomenon as a particular process restricted to a single lineage became less plausible, especially in light of parallel arguments stressing the cognitive and social sophistication of our non-*sapiens* cousins (e.g., Stiner 2017; Villa and Roebroeks 2014). However, some still object that complex traits such as imaginative and symbolic intelligence were expressed less systematically in Neanderthals (Tattersall 2017).

Problems of definition regarding what exactly is meant by the term 'behavioural modernity' persist (see Nowell 2010), but elaborating definitory alternatives is outside our scope (we'll likely end up reproducing old problems in new forms)[3]. We'll continue referring to 'behavioural modernity' with the purpose of highlighting the various investigative dimensions along which research has 'disintegrated' (see section 4), stressing available and more promising ways of rethinking the problem at hand. This disintegration of our conceptions of the phenomenon of behavioural modernity has led to the generation of new explanatory models, which we'll turn to now.

### *2.2 Models of Modernity*

Alongside asking how behavioural modernity should be detected in the archaeological record—how to characterize the phenomenon at hand—researchers have developed various models for the evolution of behaviourally modern characteristics in hominin populations. Such models differ with regards to the evolutionary trajectory of behavioural change, the geographic focus, and timing and relevant causal factors (see table 2 below).

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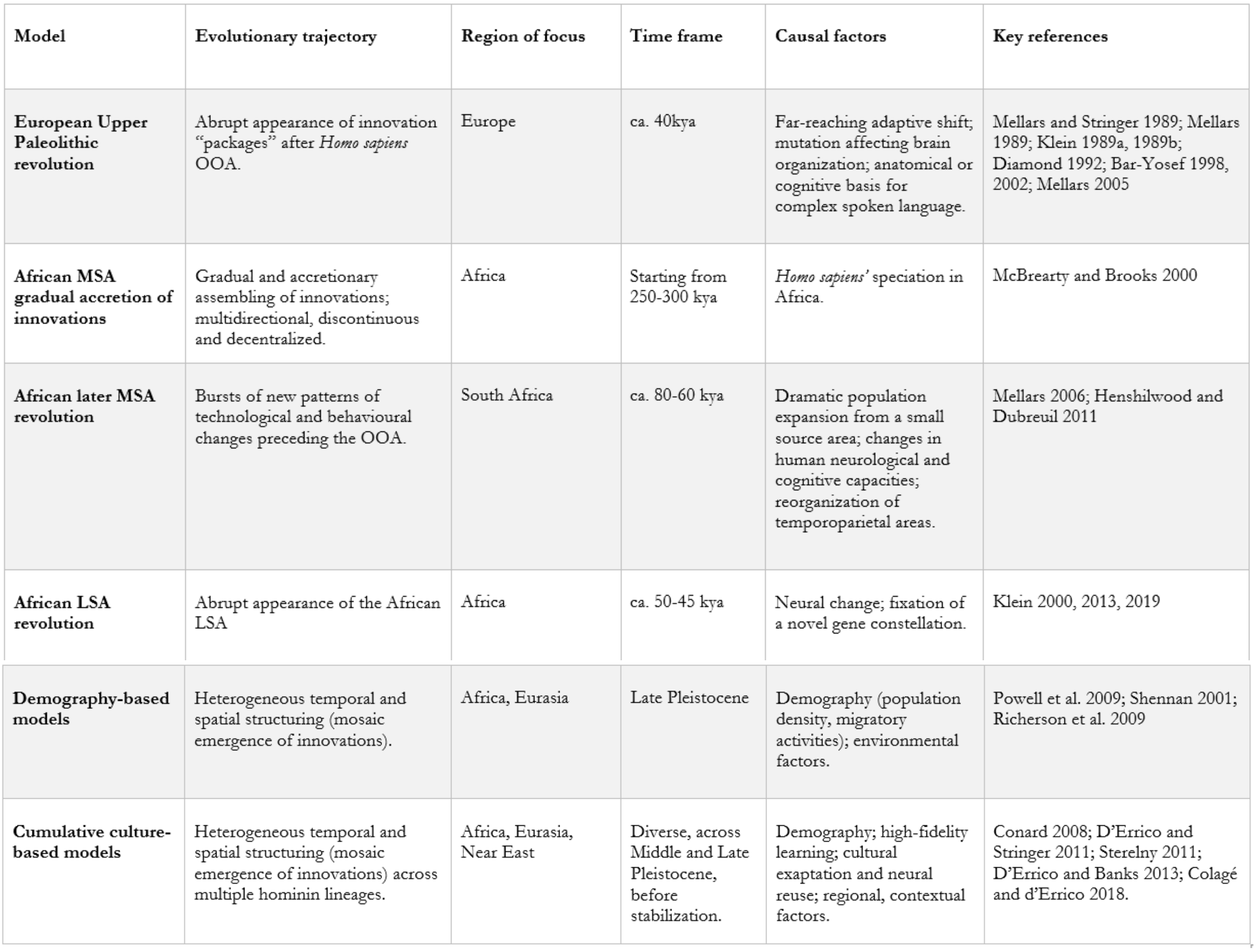
[3] As Kim Sterelny suggests,  defining behavioural modernity as falling within the range of variation of ethnographically known foragers is reasonable and neutral (personal communication).



| Model | Evolutionary trajectory | Region of focus | Time frame | Causal factors | Key references |
|---|---|---|---|---|---|
| **European Upper Paleolithic revolution** | Abrupt appearance of innovation "packages" after *Homo sapiens* OOA. | Europe | ca. 40kya | Far-reaching adaptive shift; mutation affecting brain organization; anatomical or cognitive basis for complex spoken language. | Mellars and Stringer 1989; Mellars 1989; Klein 1989a, 1989b; Diamond 1992; Bar-Yosef 1998, 2002; Mellars 2005 |
| **African MSA gradual accretion of innovations** | Gradual and accretionary assembling of innovations; multidirectional, discontinuous and decentralized. | Africa | Starting from 250-300 kya | *Homo sapiens'* speciation in Africa. | McBrearty and Brooks 2000 |
| **African later MSA revolution** | Bursts of new patterns of technological and behavioural changes preceding the OOA. | South Africa | ca. 80-60 kya | Dramatic population expansion from a small source area; changes in human neurological and cognitive capacities; reorganization of temporoparietal areas. | Mellars 2006; Henshilwood and Dubreuil 2011 |
| **African LSA revolution** | Abrupt appearance of the African LSA | Africa | ca. 50-45 kya | Neural change; fixation of a novel gene constellation. | Klein 2000, 2013, 2019 |
| **Demography-based models** | Heterogeneous temporal and spatial structuring (mosaic emergence of innovations). | Africa, Eurasia | Late Pleistocene | Demography (population density, migratory activities); environmental factors. | Powell et al. 2009; Shennan 2001; Richerson et al. 2009 |
| **Cumulative culture-based models** | Heterogeneous temporal and spatial structuring (mosaic emergence of innovations) across multiple hominin lineages. | Africa, Eurasia, Near East | Diverse, across Middle and Late Pleistocene, before stabilization. | Demography; high-fidelity learning; cultural exaptation and neural reuse; regional, contextual factors. | Conard 2008; D'Errico and Stringer 2011; Sterelny 2011; D'Errico and Banks 2013; Colagé and d'Errico 2018. |

**Table 2. Main characteristics of selected models for the evolution of behavioural modernity**.

Here are summarized six main models that are reviewed in the paper (though more have been proposed). Although overlaps and similarities are clearly possible, the distinctions are useful for detecting relevant differences in one or more of the following features: trajectory, timing, geographical focus and range of causal factors.

In the 80's and 90's, the basic picture of how and when our hominin ancestors became like us was commonly understood. According to the "Upper Paleolithic model", the path leading to the modern mind was abrupt and exclusively associated with AMHs and their arrival in Europe (Mellars and Stringer 1989; Klein 1989a, 1989b; Diamond 1992; Bar-Yosef 1998, 2002). The archaeological record of the UP , exhibiting a proliferation of new, successful technological and cultural changes suggested a "lightbulb moment" in human evolution. Early trait-list approaches on which the revolutionary scenario was based tended to suggest that innovations arrived as a 'package' during the Middle to Upper Palaeolithic transition (MP-UP). This inflection in the record was interpreted not as a biased discontinuity but as reflecting a major cognitive and behavioural breakthrough, a "creative explosion" (Mithen 1998, Renfrew 2009) so marked that some scholars argued it was probably caused by a selectively advantageous genetic mutation, occurring around 50-40 kya, affecting brain functioning and internal organization (Klein 1989a, 1989b). Others thought of changes in the anatomical or cognitive basis for spoken complex language as a plausible answer (e.g. Diamond 1992; Mellars 1996).

Within this perspective, there is an "impossible coincidence" (Mellars 2005) between *Homo sapiens'* range expansion across the European continent (following the so-called Out-of-Africa, OOA, dated at ca. 70-60 kya) and the almost simultaneous emergence throughout the Old World of technological and cultural innovations marking MP-UP transition. Resolving the coincidence led to a "single-species model" for the origin of modern behaviour, which excluded the convergent or parallel evolution of cognitive sophistication in other archaic hominin lineages (notably Neanderthals), thus accounting for the different evolutionary trajectories followed by "invaders" *sapiens* and "indigenous" Neanderthal populations, the former replacing the latter (ivi; see Villa and Roebroeks 2014 for criticism).

However, as we've seen in section 2.1, a growing body of archaeological evidence supports the emergence of key cultural innovations in Africa before the purported European creative explosion. A wealth of counterevidence has accumulated against the “revolution” scenario, that many take to favour a more gradual evolutionary picture.

According to McBrearty and Brook’s explanatory model, modern behaviour must have been the consequence of *Homo sapiens’* speciation in Africa. Therefore, a gradual accretion of innovations should be visible in the archaeological record as a result of the selective pressures leading to the emergence of AMHs (McBrearty and Brooks 2000, Marean et al. 2007). The time-lag between the origin of anatomical modernity and signals of behavioural modernity is considerably reduced within the gradualist perspective and associated with the onset of the African MSA. In explaining the expansion from Africa no genetically encoded, dramatic change is invoked: traits characterizing modern human behaviour were developed by hominin groups through cognitive and behavioural capabilities that were plausibly already in place. However, it has also been argued that the accretionary pattern could be a methodological artifact, due to mixing traits belonging to the African MSA and the European UP (Shea 2011, D’Errico and Banks 2013).

Rather than abandoning the idea of a breakthrough, some researchers placed it earlier and in Africa. For instance, Mellars (2006) has proposed that this moment should be located between 60 and 80kya in southern Africa, concomitantly with a major population expansion and with the appearance of technological and behavioural innovations in the Still Bay and Howiesons Poort industries that, he argues, sharply contrast with those of earlier African MSA sites (see also Henshilwood and Dubreuil 2011). Although invoking adaptive environmental processes as a parsimonious (and more prosaic) explanation, Mellars nonetheless argues that significant changes in human neurological and cognitive capacities can in no way be ruled out. Henshilwood and Dubreuil (2011) invoke a reorganization in modern *H. sapiens* of the temporoparietal areas implicated in higher theory of mind. Klein (2000, 2013, 2019) explicitly ties behavioural change to a fortuitous mutation or a novel gene constellation promoting the fully modern brain and the onset of the African Later Stone Age (LSA, 50-45 kya).

In parallel, however, alternative models have gained increasing consensus, radically reshaping the relevant questions and tackling different aspects of behavioural modernity. For example, the "demographic perspective" asks not how novelties emerge, but how cultural complexity is maintained (or lost) through time. Some scholars have argued that demography is a major determinant here, and that population size, density and migration activities, probably triggered by climatic and environmental dynamics, shaped the spatial structuring of cultural traits' accumulation and evolution (Powell et al. 2009; Shennan 2001; Richerson et al. 2009), thus accounting for the asynchronous appearance, disappearance and re-emergence of key innovations within the African MSA.

Others have highlighted that such demographic-based mechanisms, far from being the unique explanatory factor in the spread and maintenance of innovation (see Sterelny 2011 for the role of high-fidelity learning settings), are equally applicable to archaic hominins like Neanderthals, suggesting that their different evolutionary fate might have well been dependent on group size and rates of cultural exchange, rather than hardwired, "in-built" cognitive differences (d'Errico and Banks 2013; d'Errico and Henshilwood 2011).

Partisans of this last view, dubbed the "cultural model" (d'Errico and Stringer 2011), expand on the demographic perspective, and argue that modernity is the result of cumulative cultural evolution among populations that already had the capacity to be cognitively modern irrespective of taxonomic affiliation. Much of the cognitive prerequisites and cerebral hardware of modern behaviour were perhaps already present among the last common ancestors of Neanderthals and modern humans.

On such views, what explains the appearance, diffusion and acceptance of innovative behaviours – besides population pressures and demographic dynamics – is the ability of a society to create stable and high-fidelity learning settings within a specific, ecological and environmental context and given peculiar historical contingencies (D'Errico 2003; Zilhao 2007; Hovers and Belfer-Cohen 2006; d'Errico and Banks 2013). Here a multiple species model for the origin of behavioural modernity is invoked, contrasting the idea of a single speciation event as a main trigger. Modern traits appeared among different hominin groups and in different African and Eurasian regions, and the process of change (especially in the early phases of the MSA) was not linear nor progressive in nature, but rather followed a "mosaic" mode of evolution (see Parravicini and Pievani 2019). Here, innovations and traits appear and disappear (and reappear again in quite different forms, e.g. beads, see d'Errico et al. 2009) in an haphazard and irregular fashion, before becoming fully crystallized into a cohesive package. As for Europe, D'Errico (2003) does not exclude that contact among AMH and Neanderthals might have boosted innovation and the production of symbolic objects on both sides. What emerges then is an intricate and pluralistic picture, in which modern behaviour manifests itself as the result of multiple evolutionary trajectories followed by its constitutive traits, crosscutting hominin phylogeny.

Although this is not the only scenario available in today's approach to human cultural and cognitive evolution[4], sociocultural and demographic based models (also aided by incorporation of elements of the Evolutionary Extended Synthesis, see Kissel and Fuentes 2021) are redrawing the conceptual toolkit and investigation. Further, it is argued that such scenarios are more grounded in the available evidence compared to biologically based explanations, as they account for  patterns in the record without resorting to events that are not yet empirically

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[4] See for instance Klein's (2019) recent reconfirmation of the hypothesis of a new climate-driven gene constellation, affecting cognitive and communicative potential.

sustained (nor easily testable). For instance, it is well-established that major population growth took place in Africa before the radiation into Eurasia, likely favouring cultural accumulation (Henn et al. 2012), whereas as of today no species-wide genetic sweep just before 50kya has been found (Mallick et al. 2016).

It is clear that the notion of 'behavioural modernity' (and the whole research agenda around it, as we shall see) has undergone significant change. The causal link between modern anatomy and modern behaviour has been gradually loosened (along with the one human taxon/one cognition equation). In the case of our species, the speciation event associated with anatomical modernity (or perhaps even earlier events!) brought with it the genetically-endowed capacities required for behavioural modernity, which then slowly, in fits and starts, arose with the development of social environments scaffolding high-fidelity learning as well as sufficient demographic density to buffer information-flow and enable divided labor.

Thus, the discovery of various signals of behavioural modernity across African time and place, and of others associated with archaic hominins (both in Africa and in Eurasia), as well as new theoretical horizons, have significantly disrupted once-settled conceptions of how the transition could have occurred, and what the transition even consisted of.

## 3. Rubicon expectations

Caesar's crossing of the river Rubicon is framed as a kind of switch-point: a critical decision on his part which was necessary for the Roman Republic's fall and the rise of its Empire. Similarly, many investigations into behavioural modernity retain classificatory and explanatory practices focused on an isolated 'moment' where humans became human, or on a major proxy that should fully account for the transition. The shifts we've seen in our understanding of behavioural modernity undermine such approaches. We'll make our argument, before contextualizing it with respect to common archaeological practice.

### *3.1 Against Rubicons*

We call "Rubicon expectation" in the context of behavioural modernity the practice of establishing a boundary that is expected to provide a non-ambiguous and universally applicable benchmark for modernity, and then monitoring the archaeological record for it, thus inferring which hominin group, when and where, crossed it. Once such a benchmark for modernity is set, hominin populations/species are judged as "behaviourally modern" if their material culture meets it.

Three intertwined issues are at play that are worth distinguishing more clearly. One problem (i) involves the idea that the behavioural modernity phenomenon can be reduced to a major, big breakthrough, i.e. a key-trait model of what makes us humans different from other hominin lineages[5]. A second, related problem (ii) concerns translating this view into non-ambiguous material signatures that can be identified in different archaeological contexts. A third (iii) involves interpreting the underlying processes that produced such signatures. As seen in the previous sections these interpretations have long had an inclination towards 'switch-point' explanations, often based on biologically mediated or hardwired causal factors. Our argument, in short, is that the new evidence and models we discussed in the previous section have transformed our conception of (iii), but many of the approaches underwriting (i) and (ii) have not as yet caught up.

As we saw in the previous sections, a number of empirical findings regarding the timing, location and pace of the appearance of innovations are no longer consistent with explanations attributing them to concomitant genetic or otherwise biologically mediated processes (iii).

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[5] See Currie (2019a) for general discussion of such one-shot hypotheses.

These have pushed research towards a picture in which the mosaic appearance and disappearance of innovations in both the African and the Eurasian record is explored through multiple, interacting factors – demographic, social, cultural transmission, environmental, ecological (cfr. d'Errico and Banks 2013) – before coalescing in a stabilized and expanding human niche (cfr. Sterelny 2011; Foley 2016; Kissel and Fuentes 2018). Despite this, Rubicon expectations and classificatory approaches (involving i, ii) are retained from older explanatory strategies, falling out of phase with respect to current theoretical and empirical advancements (section 4 will develop a philosophical account of this in terms of 'investigative disintegration'). Rubicon expectations, we argue, might bias research in that they (still) implicitly depict the evolution of behavioural complexity as a demarcation problem, revolving around the identification of a major event, i.e the onset of a competence or class of features capable of telling apart modern from non-modern records, human from non-human makers. By placing the explanatory and empirical burden on the Rubicon, distortions easily arise.

We've seen how the attempt to use the European UP material record as a Rubicon for other archaeological contexts to meet failed, most significantly for empirical reasons. However, pushing back the temporal horizon for the purported boundary or focusing on one major demarcation criterion for behavioural modernity, such as symbolically mediated behaviour treated as a "golden spike", does not escape the idea that behavioural modernity requires a significant Rubicon to be crossed. Let us briefly consider this last case and the problems it poses.

Symbolic behaviour and related inventories of symbolic expression are considered by many to be the crux of modernity (Chase and Dibble 1987; Wadley 2001; Henshilwood and Marean 2003, Tattersall 2008, Marean 2015). Although what is classified as symbolic varies considerably (Kissel and Fuentes 2018), generally material items such as personal ornamentations, use of ochre (with no discernible function), artwork, and practices like burial and other ritualistic activities, are linked to symbolic expression. However, artifacts and practices are not inherently imbued with symbolism and the lack of information about the cultural systems in which those artifacts acquired meaning poses a concrete limitation, making physical symbols equally fallible indicators of cultural richness (Sterelny 2011, Kissel and Fuentes 2017, Currie and Meneganzin *forthcoming*).

Besides this, a more fundamental problem derives from what pushes the intuitive urge of identifying a Rubicon in the first place. That is, the belief that symbolic behaviour (or whatever else) captures the quintessence of being human, a trait (however complex) that should be considered exclusive to our lineage (White 1940). In the case of symbolic expression, this seems evident in Henshilwood and Marean (2003) equating the expression "modern human behaviour" with "fully symbolic sapiens behaviour" (p.644). This reproduces an old methodological problem. Replacing the old trait-list with an archaeological golden spike does no more than recreate the form of circular reasoning previously criticized regarding the UP 'revolution': if we define the capacity for symbolism as an exclusive human trait – being it, again, empirically derived from the material record of AMHs – we already know which assemblages will pass the modernity test.

Nonetheless, recent findings (although not without controversy) suggest that archaic populations were capable of symbolic expression, blurring the purported boundary between symbolic and non-symbolic species. Early glimmerings of possible instances of symbolic material culture (like abstract engravings and carvings) are reported at very ancient sites (800 - 300 kya, according to Colagè and D'Errico 2018), suggesting that the capacity for symbolic thought may have deeper phylogenetic roots . One ancient evidence of symbolic expression has been attested from an engraved clam shell from Trinil (Java), dated at ca. 540-430kya and attributed to *Homo erectus* (Joordens et al. 2015). More significantly, different European Neanderthal sites contain traces that have been suggested to be symbolic in nature. These include burials, pigment use, personal ornamentations, collection of natural rare items and possibly cave art (Zilhao 2007; Hovers and Belfer-Cohen 2006; Villa and Roebroeks 2014; Hoffman et al. 2018). When these expressions are not discarded as illegitimate or ambiguous in their intentions (probably because their evaluation is, in some cases, highly dependent upon the AMH-derived yardstick, i.e. the idea there is only one way of being truly symbolic), moving targets for behavioural modernity easily arise.

Strictly related to the issue of circularity is a second methodological problem, which we take to be even more pressing: capturing change in a mosaic-like transition. If the evolution of modern behaviour and complexity does not follow a unique path of development, but takes place along multiple trajectories, defined by different times, modes, locations and including various combinations of traits, then the processual nature of the phenomenon makes Rubicons unable to snap-shot a clear dichotomy between modern and non-modern assemblages, simply because no harsh dichotomy is to be expected. This also means that every temporal 'photograph' in the evolution of a complex feature such as symbolic expression must be interpreted from an evolutionary standpoint, i.e. bearing in mind that early glimmerings – or even evidence associated with other hominin groups – are expected to be different from Late Pleistocene or even modern-day manifestations. Thus, instead of seeing proxies of behavioural modernity as indicators of whether we have behavioural modernity or not—classifying the relevant population as 'archaic' or 'modern'—they are instead data relevant for understanding the mosaic of processes which eventually enabled cultural, informational and demographic stabilization.

This brings us to the explanatory dimension. No proxy in itself, not even symbolic expression, can alone have special significance. Placing the Rubicon when symbolic manifestations already show a stabilized signal (as Klein 2019 seems to do in recognizing an abrupt inflection in the record, marked by the appearance of the LSA in Africa, and simultaneously, of the Eurasian

Upper Palaeolithic) is not particularly informative nor decisive for assessing questions surrounding behavioural modernity, if it is not subsumed under the question of which mechanisms allow for the retention and proliferation of those expressions, as well as for the toleration of their costs. This does not mean downplaying the importance of detecting manifestations of symbolic expression (or other traits) in the archaeological record: rather, explanatory efforts should be directed at the mechanisms behind the transition, not its archaeological symptoms. As Ames et al. (2013) effectively put it:

> Shifting the focus to identifying broader patterns of human adaptive strategies in social and ecological context still depends on our ability to document fluctuations in material culture through time and space, but it differs from the practice of monitoring the presence/absence of traits by singling out the range of behavioural strategies employed as the target of analysis, as opposed to trying to figure out whether or not a given assemblage passes the modernity threshold. In a way, this is an operationalization of the recognition that modern behaviour is a mosaic concept that needs to be interpreted as a function of its wider social and ecological contexts (Ibid. 36)

Thus, on our view, the continued use of Rubicons to demarcate behaviourally modern from non-modern hominins represents an outdated and misplaced expectation that is ill-fitting with respect to current knowledge and awareness of the complexity of the phenomenon. However, isn’t it the case that linking material culture to social and cognitive capacities is common in archaeology? In the next subsection, we’ll further contextualize our position.

### *3.2 Archaeological business-as-usual and Rubicons*

Behavioural modernity, as we’ve seen so far, is identified in the record via archaeological assemblages taken to be signals of complex cognitive and social traits. This, in many ways, is archaeological business-as-usual. Archaeological categorization typically identifies cultural groupings via signals in the archaeological record: the ‘Clovis peoples’ identified by arrowheads across North America being a famous example. In paleoanthropological contexts, such categories are typically highly theoretical, based on ideas of the minimal cognitive, technological and social capacities required to construct such material remains (Currie & Killin 2019, Pain forthcoming). Such inferences often aim to identify the latest time that the capacity is present. So, hominin groups with, for instance, ochre use or beaded shells (keeping in mind the ambiguities of artifact significance that we mentioned) are categorized as behaviourally modern because it is taken that such material items signal symbolic expression. This approach has led to focus on a series of ‘Rubicons’ which various groups have taken to have crossed or failed to: archaeologists examine assemblages, identifying some groups as modern and other groups as not. Rubicons also set the significance of finds: discovering, say, ochre use in earlier times, or at wider ranges with respect to models’ expectations, are treated as highly surprising and worthy of publication in prestigious journals. As such, Rubicons do a lot of work structuring archaeological investigation.

In light of the shifting research agenda for behavioural modernity, however, we think Rubicon expectations are unproductive and distortive lenses which actively undermine research. Recent models of the emergence of behavioural modernity understand it as a ‘process’ rather than an ‘event’ (Kissel & Fuentes 2018), or as ‘threshold’ in the bandwidth and fidelity of expertise flow (Sterelny 2011). We could describe it as an ‘emergent property’ that belongs to a social group and which arises (and becomes visible) from the collaborative functioning of a system of interrelated factors (biological, cognitive, social-demographic, cultural). More specifically, we could envisage feedback systems of interactions according to which cultural practices can have direct effects on the cognitive capabilities of hominin populations and the neural substrates of individuals, constructing developmental environments to which future generations are exposed and amplifying learning capacities (see also Heyes 2018).

Despite differences, recent approaches hold in common the idea that the material record does not simply track innate capacities – what Sterelny (2011, 2017) calls the ‘simple reflection model’ and whose ‘bottom-up-only’ direction of dependence is criticized by Colagè and d’Errico (*i.e.* the idea of a straightforward chain from genetic changes, to brain anatomy and physiology, to cognitive skills, to the package of cultural innovations that make us human, cfr. Colagè and d’Errico 2018). Rather, signals in the record showing the preservation and expansion of innovations reflect the culturally evolved and maintained epistemic niche of human groups. As such, inferring from the absence of material symbolism (say) to the fact that it did not exist and hence to archaic capacities—categorizing that group as non-behaviourally modern—is a mistake. It may rather reflect contingencies in that group’s ecological and cultural context, not innate capacities. More careful use of proxies, such as simply being signals of the latest possible presence of the capacities (Killin & Pain 2021) are also undermined. On these models, we’re not primarily interested in identifying when the innate capacities may have arose (as the basic prerequisites might have a deeper evolutionary history, and they’re potentially spread across many hominin taxa), but in mosaic patterns of loss and stabilization.

Further, identifying particular finds as significant in virtue of, as it were, being in the wrong time and place is not particularly informative, nor does it meet the explanatory objectives of today’s research. If we’re looking for a Rubicon, then finds in earlier times or different locations are anomalous; however, if we’re expecting a threshold effect they are not.

## 4. Disintegration

It might be tempting to read the scientific developments thus far via hum-drum processes of hypothesis-testing. The hypothesis that behavioural modernity consists in changes in intrinsic cognitive capacities arising as the result of a genetically-mediated ‘quantum leap’ in a localized population and region (e.g. Mellars and Stringer 1989, Bar-Yosef 1998, Klein 1989, 2000, 2013, 2019) came under increasing empirical pressure as new paleoanthropological and archaeological data came online, leading to the development of new hypotheses which better accommodated the picture's complexity. There is no doubt something to this: such hypotheses have indeed been tested and put under pressure (cfr. Mallick et al 2016); but in this section we'll argue for a different reading. The new data doesn't simply test hypotheses, they also transform our conception of target phenomena, the investigation has 'disintegrated', and this has important consequences for the kinds of explanations we should prefer and the epistemic structure of the investigation.

We'll foreshadow our account by responding to two immediate worries. First, you might think the term 'disintegration' is a bit dramatic: as we'll discuss below, we've not had to abandon swathes of empirical data relevant to behavioural modernity, and indeed in 5 we'll argue in defence of retaining the notion itself (once adequately updated)[6]. But disintegration comes in degrees[7]. We've shifted from behavioural modernity being an integrated package of cognitive traits aligned with a particular set of assemblages, to something much more disparate and complex in its explanatory dimensions. It is this partial process that our account of disintegration seeks to capture.

Second, you might worry that the driving thought—that new conceptions of phenomena can change what counts as explanatorily adequate—is trivial. If we're convinced of the context-sensitivity of explanation, then of course changes to context involve changes in explanatory adequacy. But this is too quick: investigative disintegration involves more than changes to

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[6] We can indeed imagine more dramatic forms of disintegration, for instance cases in which it is no longer possible to save anything from the previous understanding of the target phenomenon (we would intuitively call such cases "disruption" or "dissolution" of the target phenomenon). But exploring them would bring us beyond the scope of the current paper.

[7] It might help the reader to space the word out: *dis-integration*.

what explanation we want, it also involves changes to an investigation's epistemic structure, and this can have important consequences for, for example, the significance of new finds (we'll discuss some of these upshots in section 5). Beyond explanation's context-sensitivity, we are interested in the *dynamics of explanation*, something Max Dresow has recently highlighted:

> [the dynamics of explanation illuminates] the temporal dimension of explanation *considered as an open-ended and collaborative process.* Here we are not concerned with single explanations (or at least we needn't be), but rather with teams of explainers working jointly or in competition. (Dresow forthcoming, 2, italics in original)

As Dresow points out, the dynamics of explanation lead us to focus on the relationship between how explanations unfold and the investigative contexts in which they are embedded. For behavioural modernity, new empirical findings and new theoretical tools have radically reshaped explanatory expectations and goals, which we'll characterize in terms of 'investigative disintegration': new understanding of the phenomenon, driven by new data and new interpretations of already available evidence, has reshaped the kind of questions we're asking and the kind of answers we want. Following Dresow, the dynamics of explanation are not simply about *explanation*, but about how explanatory expectations interact with, and are shaped by, efforts to characterize phenomena.

To capture the notion of investigative disintegration we'll turn to Alan Love's work.

### *4.1 Problem Agendas*

The notion of a *problem agenda* is useful for framing investigative disintegration. A 'problem agenda' is, in effect, a list of questions unified not by a theoretical perspective nor method, but by a phenomenon of interest. As Love puts it: "A problem agenda… is a "list" of interrelated questions (both empirical and conceptual) that are united by some connection to natural phenomena” (Love 2006, 877). The agenda sets the role that various explanatory and evidential components play in understanding that phenomenon, particularly setting *explanatory adequacy*. That is, what kinds of answers count as a passable answer to the question at hand—if you want, which hypotheses are *relevant*. Further, this assigns ‘explanatory burden’ to some components of research over others.

> Because general criteria of explanatory adequacy provide structure to the explanatory burden associated with problem agendas, this epistemological account has the resources for ascertaining what disciplinary contributions are prerequisites for adequate explanations. The structure of a complex problem set derived from making the criteria of adequacy explicit highlights what different conceptual resources must be drawn upon to produce an acceptable explanatory vantage point (Ibid, 878).

Research into the deep past is by its nature multidisciplinary and integrative: the traces of past events and trends are often scarce, distorted and varied, requiring scientists to draw together a wide range of techniques, methods and theoretical resources to integrate the varied evidence available from historical records (Chapman & Wylie 2016, Currie 2018). Problem agendas are a useful way of understanding the various roles data and theory can have in these complex investigations. To illustrate this through a nonhuman example, let’s dip our toes into discussion of the evolution of obligate grazing amongst ungulates in the later Miocene (based on Janis 2008).

The basal diet of ungulates is based on browsing, consuming the leaves and stems of plants, as well as fruit. Although grass arose earlier, it didn’t become an extensive feature of global biota until the later Cenozoic (say, 25ma). As grass spread, so also did grazing in ungulates as they adapted to the new environments. Obligate grazing arose in *Equids* in North America and *Bovidae* in Africa. A relevant phenomenon of interest is variation in size between the obligate grazers, horses and bovids, and the browsers which includes giants such as rhinoceros, giraffe and elephant. In short, browsers are able to attain larger sizes than grazers: why?

Identifying phenomena like size differences between grazers and browsers generates problem agendas, which we can understand as setting the role various data and theory play in the investigation. First, some evidence, as it were, *frames* the investigation: data about the timing of grassland spread and of related radiations, as well as general comparisons between browsing and grazing strategies. Second, many threads play a role in *characterizing* the phenomenon at hand: establishing the uniqueness of bovids and equines involves phylogenetic analysis, establishing the difficulties of grass consumption and digestion, and the particular strategies adopted by various ungulates. Framing and characterizing the phenomenon help set explanatory adequacy but does not meet it. An explanatorily adequate answer to our question must identify what is different about obligate grazers in contrast to other ungulates such that they are limited in size[8].

For instance, consider the role of highly hypsodont molars. *Hypsodont* teeth have high crowns and enamel reaching beyond the gum-line, and are commonly understood as an adaptation for dealing with abrasive vegetation. However, "not all hypsodont ungulates are grazers, as the silica contained in grass is far from the sole abrasive element in a herbivorous diet" (Janis 2008, 29). Because hypsodoncy cannot tell between grazers and other ungulates, it alone doesn't meet explanatory adequacy—cannot carry the *explanatory weight*—of the problem agenda. However, it can play a role in framing and characterizing by helping identify mixed dietary and grazing strategies when they arise in the fossil record. What is needed for adequacy is identifying a relevant difference between the various lineages.

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[8] This in part relies on *contrastive* accounts of explanation, see for example Lipton 1990.

For instance, consider Clauss et al (2003)'s explanation. Obligate grazers typically use fore-gut digestion and are ruminants, an adaptation allowing for the digestion of grasses. Ruminants rely on delaying the passage of digestion, in order to have digesta available for re-chewing. Thus, digesta passage-time in ruminates is slower than in hindgut fermenters, and passage time scales with body-size. So, the larger a ruminant becomes, the longer digestion takes. This limits body-size because the efficiency by which acetic acid is converted to methane and carbon dioxide breaks down at longer digestion times. So, because hindgut fermenters generally have quicker digestion, they can afford larger sizes than foregut fermenters. Clauss et al's explanation is adequate due to identifying a relative difference between hindgut and foregut fermentation, capturing why the former have size constraints the latter do not.

Let's apply the example. We can understand a problem agenda as structuring the various roles data, evidence and theory plays in an investigation. An agenda picks out a particular phenomenon (that hindgut fermenters attain larger sizes than foregut ruminants) and in virtue of this some information takes on characterizing roles (size patterns and phylogenetics amongst ungulates), some framing roles (the various mechanisms and efficiency of digestive strategies) and others the explanatory burden set by explanatory adequacy (the constraints foregut digestion place on size). It doesn't follow from this that Clauss et al's explanation is right, simply that it is explanatorily adequate given the problem agenda.

Problem agendas can be highly sensitive to both empirical context and explanatory interests. Switching our question, say, to the timing of the arisal and spread of obligate grazing, restructures the investigation: adequacy now calls for capturing why ten million years ago, and not earlier, ruminants arose. But this should be no surprise to philosophers used to the context-sensitivity of explanation. What we learn from Love's framework is that it is not simply explanatory adequacy that shifts with context, but the roles data and theory play. Further—and this is critical for investigative disintegration—learning new things about the underlying phenomenon can radically reshape explanatory adequacy and the agenda at large.

### *4.2 Investigative Disintegration*

As mentioned in the introduction, philosophers of science have rightly shifted from general accounts of unity and disunity to accounts of local integration and independence across several dimensions (data, evidence, hypotheses, institutions, etc…). Less attention has been paid to what happens when phenomena of study turn out to be far different from once thought; when investigations 'disintegrate', a process which has plausibly occurred for behavioural modernity. In this section, we can characterize one form of investigative disintegration by drawing on Love's machinery. In short, new information about the nature of the phenomenon[9]—shifts in how it is characterized—can dramatically reshape investigation. This has consequences both for what constitutes an adequate explanation of behavioural modernity, and how we should read it from the archaeological record.

Let's remind ourselves, then, of how the phenomenon of behavioural modernity has changed, before characterizing the notion of disintegration abstractly.

We began tackling a relatively clear archaeological signal, the apparently sudden emergence, in the European UP, of a rich assemblage associated with symbolic expression, complex tool-use and so forth. This phenomenon shaped a problem agenda. First, the signal frames the investigation by discriminating between the biological emergence of *H. sapiens* and the appearance of behavioural modernity. Second, the distinction between anatomical and behavioural modernity sets relevant questions: what explains the ca. 150kya gap between our species' evolution and our becoming behaviourally modern? Further, why was the emergence

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[9] By 'phenomenon' we mean something similar to Bogen & Woodward (1988): a recurrent pattern inferred from data.

so sudden? Third, such questions drove a set of expectations: the explanatory weight is carried by a saltationist, often genetically-mediated mechanism involving a set of key innovations in a local population.

However, over twenty years anomalies arose which didn't simply undermine saltationist hypotheses, but reshaped the phenomenon, problem agendas and standards for explanatory adequacy. The discovery of increasingly diffuse, often partial, aspects of the assemblage identified with behavioural modernity earlier in the record challenges a saltationist picture and the idea that we should explain the origins of a 'syndrome', but so too does it challenge the usual way of understanding the distinction between behavioural and anatomical modernity. Instead of marking a genetic transition, we instead see a mosaic of potential precursors. Explanatory adequacy shifts from requiring a story about a single, localized origin, to asking after stabilization. Models of learning, social organization, demographics and niche stabilization take on explanatory weight previously carried, under many instances of "revolution" scenarios, by genetic or biological evolution. Again, as seen in the discussion of the evolution of obligate grazing, it doesn't follow from this that such specific models are inevitably right, but that they are explanatorily adequate[10]. On this basis we can characterize investigative disintegration abstractly:

Investigative disintegration, in such instances, occurs when: (1) the characterization of a phenomenon changes sufficiently for (2) different components of the problem agenda to take on explanatory weight[11].

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[10] Note also how this differs from a simple case of epistemic pluralism. For pluralism to occur, under this perspective, multiple accounts must equally satisfy criteria of explanatory adequacy. But this is not the case of old and more recent Rubicon-based approaches, as seen above. There is however room for much pluralism regarding the nature of the stabilizing processes underwriting modernity.

[11] It might be tempting to see this as the arisal of a new problem-agenda. We don't think much hangs on how precisely we delineate problem-agendas, context-sensitive as they are.

Note that our definition of investigative disintegration doesn't specify which factors might change how phenomena are characterized: we suspect a wide variety of influences could be at play, and want to avoid overgeneralizing from our example. For it is likely idiosyncratic. Investigation of behavioural modernity operates under 'epistemic scarcity' (Currie forthcoming): like many studies of the deep past, data is rare, fragile and difficult to manage. In virtue of this, phenomena are often highly sensitive to new incoming data. This scarcity in part explains how expanding paleoanthropological and archaeological discoveries (along with new theoretical frameworks) could so thoroughly reshape the epistemic landscape. Investigations with more systematic and manageable data could prove more intransigent.

Moreover, we're concerned here with forms of disintegration involving shifts in phenomena. Specifically, new ways of characterizing the phenomenon, driven by new finds and theoretical innovation, led to very different requirements in explanatory adequacy. But this is likely but one way the dynamics of investigation might shift. Other examples may include cases where changes in theory play a central role, say, but we'll leave that more expansive discussion for later work.

There are similarities between the phenomenon we highlight here and older systems within the philosophy of science. For instance, new evidence pertaining to behavioural modernity could be aligned with Kuhn's 'anomalies' (Kuhn 1962), and the shifts in our conception of behavioural modernity might be aligned with shifts in Lakatosian 'cores' or progressive or regressive problem shifts (Lakatos 1976). It may be that what we pick out here could be captured with this machinery. However, there are important differences: both Kuhn and Lakatos are significantly more systematic than we wish to be.  For instance, comparing a Kuhnian 'paradigm shift' to investigative disintegration reveals significant differences between them. We'll briefly highlight two.

First, differences in the degree of disintegration: because paradigms holistically structure research programs they appear to be an all-or-nothing affair, while the finer-grained structure afforded by disintegration can better capture the actual dynamics of research. This affords side-stepping long-toothed worries about incommensurability while nonetheless allowing critical engagement with the dynamics of research. Although changes in how behavioural modernity is conceived has not led to a breakdown of communication or method, we've argued that it has involved certain practices—particularly those related to the categorization and significance of new finds—dragging behind the epistemic purposes of the reforming agenda.

Second, the scope and organizing principles of research agendas differ from paradigms. It isn't clear that behavioural modernity is anything like a paradigm (or the core of a research program for that matter): problem agendas tend to come into being in piecemeal, messy ways and tend to focus on significantly narrower targets than paradigms. More importantly, as research agendas focus on phenomena and how scientists characterize these, they are more appropriate for behavioural modernity than more 'theory-centric' approaches. This is simply because in this instance it has not been changes to wide-scale theory, nor evidence undermining such theory, that has ignited the change: it is primarily how new finds (and the reappraisal of old ones) have reshaped how the phenomenon is characterized.

Having said this, we are open to understanding these notions as ways of (as an anonymous reviewer nicely put it) 'rescuing the morals of Kuhn'[12]. In a sense at least, understanding investigative disintegration is in step with understanding anomalies and their subsequent revolutions insofar as both are fundamentally interested in how unexpected discoveries shape the dynamics of research. The crucial difference, we think, is that investigative disintegration

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[12] See Havstad & Smith (2019) for an excellent approach to rescuing the morals of Lakatos.

follows the crucially local, practice-oriented and dynamic turn of recent philosophy of science (a turn which, we've briefly suggested, is for the better, at least in this context).

There is a certain tension in our use of the term 'disintegration': after all, it was the integration of new data which proved so thoroughly transformative. But this is what we should expect. Integration at some level can lead to disintegration at another, as science's epistemic tapestry is warped around new discoveries, analytic techniques and models. This suggests a positive epistemic role for disintegration: too-closely integrated research programs might well lead to a too-strict, restricted, investigation. Such investigations are likely blind to alternative hypotheses due to a too-conservative focus (Stanford 2006, 2019, Currie 2019b, Schneider forthcoming). Our account then provides an additional nail in the coffin of the "jigsaw puzzle-metaphor", often invoked to (mis)represent archaeological practice (see Chapman and Wylie 2016). The metaphor involves conceiving research progress as filling gaps and finding new pieces of information that will fit pre-existing schemas. Rather, empirical findings concerning behavioural modernity have, in an iterative fashion and with much theoretical innovation, led to the re-conception of what the phenomenon itself is, how it should be categorized, and how we should explain it.

We don't wish to derive more general normative claims about the role of disintegration in the dynamics of science, as there well may be more disruptive cases where target phenomena are completely dissolved and research achievements are not preserved (these may be instances analogous to Kuhn-loss, see also footnote 6; in the following section we'll explain why this is not so for our case). Instead, in less dramatic circumstances, via 'shaking up' the research program, disintegration can lead to bursts of new ideas: something we're witnessing for behavioural modernity. Thus, our position is not merely a description of the dynamics of research, there is also scope for understanding investigative disintegration as *progressive*, at least in the instance we've applied it to.

## 5. The fate of ‘behavioural modernity’

In light of its mosaic emergence, the disparateness of its proxies and troublesome baggage both from Eurocentric origins and the hunt for Rubicons, we might be tempted to abandon ‘behavioural modernity’ altogether. Shea (2011), for instance, attacks it for being qualitative, essentialist, and replicating the binary dichotomy between modern and nonmodern states. However, we think the abandonment of the notion should be resisted for three reasons.

First, Shea proposes to focus instead on ‘behavioural variability’, defined as a “measurable quality of all human behaviour expressed in terms of modality, variance, skew, and other quantitative/ statistical properties” (ivi, p. 2). However, it is not clear how a focus on behavioural variability would avoid recreating old operational problems in a different context: to measure variability, some units of input will have to be counted and what units to consider will need to be decided, thus risking to reintroduce the flaws of the old dreaded trait list approach and research agenda.

Second, even after rejecting the problematic legacy of behavioural modernity, there is still something to be explained, making the adoption of a new notion too quick a move (perhaps even unnecessary). Shea seems to treat the idea that a relevant transition might have occurred as illegitimate (as reflected in the title of his paper, “*Homo sapiens is as Homo sapiens was*”). The archaeological assemblages associated with hominin activity 300-200kya display a radically different pattern of cultural and ecological flexibility, complexity and density to those 100-50kya. Explaining ‘behavioural modernity’ is to explain those genuinely puzzling differences in the record, despite the radical changes in how they are now conceptualized.

Third, there is a potential unity to the explanations which are emerging, as indeed we might expect from some cases of investigative disintegration. That unity is not found in any predefined cultural expression or assemblage. There is not necessarily a particular signature or set thereof, be they ‘golden spikes’ or a trait-list, associated with behavioural modernity. But contingency and diversity at the level of cultural assemblage doesn’t undermine another kind of unity.

As we’ve seen, contemporary explanations point to demographic scale and sociocultural innovations (such as high-fidelity and high-volume social learning) as being *necessary* for the expression and stabilization of diverse hominin expressions. If they continue to bear out empirically, we should conclude that it is *those processes* which explain (or perhaps even constitute) behavioural modernity. The new explanations, then, are unified via pointing to a *set of cultural and demographic processes* regardless of the particular cultural and technological expressions they underwrite, the taxonomic affiliations at hand, or the material records that signal them.

This leads us to two final points. First, we’ve argued that Rubicon practices and expectations in classification (classifying assemblages as ‘modern’ or ‘archaic’, for instance) are wrong-headed. This is due to the progressive disintegration of the problem agenda—from conceiving of behavioural modernity as a shift in innate capacities to a shift in epistemic niche—and the complex nature of the target phenomenon, that Rubicons (otherwise not infrequent in archaeological investigations) are inappropriate for this kind of study.

So, what should we do instead? Our argument in no way implies that discoveries in fieldwork are unimportant for filling out our picture of the emergence of behavioural modernity. Rather, it suggests such discoveries play a different role than previously thought. New finds do not shift when purported Rubicons were crossed, but instead help test and enrich models of how the mosaic emergence of behavioural modernity occurred and which conditions allowed for such threshold effects to become visible. As we’ve said, categorization in paleoanthropology is not theoretically innocent, but rather reflects the presumed mechanisms of evolutionary and cultural change. As we underlined above, finds and assemblages should be interrogated with respect to how they document cultural changes and the underlying mechanisms at a regional scale, not as reflecting shifts in in-built capacities.

Second, Rubicon-based practices often govern what counts as significant in archaeology: it is discoveries which expand Rubicons that deserve special place in high-profile prestige journals, for instance. Finds which are earlier than we expect, or from unexpected geographical regions, take on the most significance as they shift “implicit” Rubicons or encourage revising outdated assumptions. Even within the processual understanding of behavioural modernity, finding precursors may be surprising: discovering, say, a flourishing musical tradition complete with tuned instruments 150kya would be quite remarkable. But if we think behavioural modernity is a mosaic and eventually stabilizing process reliant on demographic and cultural innovations, earlier precursors become less anomalous and their significance should be treated differently. Ultimately what matters is enriching our picture of how those processes were enacted across different contexts.

## 6. Conclusion

We’ve aimed to both provide an analysis of how investigations of behavioural modernity have been reshaped over thirty years, and cover a hitherto underexplored feature of the dynamics of scientific research. Regarding the latter, where philosophers have analysed how new research agendas and repertoires form and stabilize, we’ve considered processes of disintegration: how evolving conceptions of phenomena can reshape what counts as explanatorily adequate for a research agenda. Regarding the former, behavioural modernity’s mosaic, partial and incremental nature undermines the still-common archaeological practice of categorizing assemblages and complex, transitional phenomena via strict Rubicons.

During periods of destabilization and disintegration various scientific practices shift at different rates. We have analysed a disintegration process that began decades ago and it is still ongoing, with some practices not being aligned with the current problem agenda. We have also suggested – although we leave a more thorough examination to a future project – that investigative disintegration, in the form we analysed (as shifts in target phenomena), is a phase in the dynamics of research that can play a positive epistemic role, fostering new conceptual reorientations and eventually new forms of unity to explanations.

There is much more to be said about investigative disintegration. As we’ve suggested, our example is likely idiosyncratic: examination of other cases is likely to demonstrate different dynamics and may be less focused on shifts in phenomena. Further, we’ve said nothing about the role of disciplinary and institutional shifts in disintegration, nor about broader social factors in driving scientific change. As for behavioural modernity, although the concept should be understood as a threshold phenomenon rather than a discrete revolution, the notion still plays a critical role in holding together research agendas surrounding the evolution of our species.

On our view, the new picture emerging of the evolution of *H. sapiens* has already put in place ways of rethinking the purpose and practice of how we identify and conceptualize behavioural modernity in the first place – a picture that points towards a complex and contextualized interplay between demographic and cultural factors, as well as ecological and biological dimensions, that are responsible for the stabilization and flourishing of ‘modern’ human lifeways and diversity.

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## Acronyms

**AMHs** Anatomically Modern Humans

**LSA** Later Stone Age

**MSA** Middle Stone Age

**MP-UP** transition Middle to Upper Palaeolithic transition

**OOA** Out of Africa

**UP** Upper Palaeolithic

# 4.

# Implications of archaic hominin admixture

## Were Neanderthals and *Homo sapiens* ‘good species’?

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## Abstract

Prior to the advent of whole-genome sequencing in ancient humans, the likelihood that *Homo sapiens* and Neanderthals admixed has long been debated and hypotheses of hybridization derived from phenotypic assessments only. Today, evidence for archaic hominin admixture is being documented in an increasing number of studies, expanding the evidential basis of the debate on whether *Homo sapiens* and Neanderthals merit separate specific taxonomic status.

Here we argue that while new evidence has provided us with a finer-grained picture of ancient demographic dynamics, it does not yet justify merging the Neanderthals in an expanded concept of *Homo sapiens* or abandoning specific taxonomies. We approach this issue and the apparent conflict between molecular and morphology-based taxonomies from a diachronic perspective on lineage divergence, highlighting how different taxonomic properties are expected to arise at different points in time, and from an integrative perspective on different species conceptions and delimitation criteria. We argue that in light of similar “invasions” of the genome among other animal taxa, full reproductive isolation as the final, litmus test for distinct species status should be rather considered a biologically misplaced expectation. We therefore suggest that specific nomenclature should be justifiably applied also in human paleogenomic publications, maintaining congruence with zoological literature.

We finally consider and problematize recent suggestions that human evolutionary diversification should now be best represented by a ‘braided stream” or a network.

## Keywords

Admixture; *Homo sapiens;* interbreeding; Neanderthals; paleogenomics; species delimitation; taxonomy.

Over the past decade advancements in ancient DNA extraction and analysis have started to weigh in on long-enduring questions in paleoanthropology (Pagani et al. 2016; Nielsen et al. 2017; Wolf and Akey 2018, Bergström et al. 2021). Admixture, the exchange of genetic material between genetically divergent groups, is an increasingly documented phenomenon among animal taxa and almost a commonplace among plants, and today is considered as a valuable source of new variation and diversification (Arnold and Kunte 2017; Edelman et al. 2019; Taylor and Larson 2019). In the pre-genomic era, the possibility for interbreeding and admixture to occur among hominin species (notably, among Neanderthals and *Homo sapiens*) – as well as their extent and role in evolutionary histories – has been the subject of long and heated debates, mostly due to lack of consensus on the empirical expectations for what hybrid morphologies may look like (Ackermann et al. 2010, 2019). For much of the XX century, the controversy has centered around the confrontation between the single-origin and the multiregional models of *Homo sapiens'* evolution (reviewed in Stringer 2002; Manzi 2012). The former viewed modern humans as a recent species arising in Africa and replacing "archaic" populations during its range expansion across Europe, with little (if any) hybridization; the latter hypothesized regional continuity between archaic and modern populations and global and long-standing gene flow. Now in the post-genomic era, interbreeding has started to break also into human evolutionary paleoanthropological studies as a no longer negligible phenomenon, calling for an update of the recent African origin model – still supported by data and regarded as the consensus view (Stringer 2014; Galway-Witham and Stringer 2018) – and thus bringing *Homo sapiens*' evolution into line with that of other closely related zoological taxa.

Anthropologists have been debating over whether *H. sapiens* and Neanderthals form truly distinct species ever since the discovery of the latter (Madison 2016). This controversy hinges on the wider debate on species concepts and is exacerbated by its treatment in most scholarly publications where today the problem of species designation is not always explicitly addressed. In particular, it is often eschewed by paleogeneticists, who rather refer to Neanderthal and *Homo sapiens* as intermixing 'populations' or 'archaic groups' (Gibbons 2011; Bergström et al. 2021), while physical anthropologists emphasize morphological and developmental differences in favour of distinct species status (Harvati 2003; Tattersall 2007; Stringer 2014; Wood et al. 2016).

In section 1 of this paper, we briefly review the impact of evidence of archaic interbreeding in adding new depth to the picture of the interactions among *Homo sapiens* and Neanderthals, suggesting that what we are witnessing is an increasingly fine-grained scenario of demographic complexity. Section 2 will address the problem of species delimitation in a paleontological context that benefits from the availability of ancient molecular data. We approach the issue from an integrative perspective on various evidence and species concepts that value different delimitation criteria as complementary rather than alternative. We suggest that the fixation of taxonomically relevant properties must take into account divergence history and that "full reproductive isolation" as the final word on species status is a biologically misplaced expectation.

Finally, section 3 will discuss the implications of hominin admixture regarding whether we should move beyond phylogenetic trees and switch to network-like or "braided" representations of hominin evolution.

## 1. Neanderthal - *H. sapiens* admixture and ancient demographic complexity

Paleogenomic studies are playing a fundamental role in expanding and reframing our understanding of human evolutionary history, providing new insights on how admixture has shaped past and present patterns of genomic variation.

The first draft sequence of the Neanderthal genome revealed approximately 2% of Neanderthal ancestry in present-day Eurasian populations (Green et al. 2010; Prüfer et al. 2014). Although it has been recently shown that smaller amounts of Neanderthal ancestry are also present in African individuals (Chen et al. 2020), probably a consequence of a later back-to-Africa migration, the almost ubiquitous signal outside Africa has been interpreted as the result of a major admixture event between early modern humans and Neanderthals, that likely took place in the Middle East, before the former expanded in Eurasia and diverged in different populations, between ca. 65 and 47kya (Sankararaman et al. 2012). In eastern Eurasia the proportion of Neanderthal ancestry seems to be higher compared to western Eurasia (where it is an approximately one fifth to one tenth lower relative proportion) (Wall et al. 2013). Multiple pulses of admixture have been proposed (Vernot et al. 2015), but dilution by groups carrying little or no Neanderthal ancestry is also a plausible explanation (Lazaridis et al. 2014; Bergstrom et al. 2021).

The genetics of early modern humans is also revealing diverse patterns of interactions with archaic hominins and contributions to later populations. For example, the roughly 45.000-year-old modern human male from Siberia (Ust'-Ishim) and the 42.000-37.000-year-old individual from Romania (Oase 1) both show signals of Neanderthal ancestry (Fu et al 2014; 2015). The Ust'-Ishim individual, although carrying a similar amount of Neanderthal ancestry as present-day Eurasian, presents substantially longer segments, indicating a Neanderthal gene flow event 7.000-13.000 years before he lived. Oase 1 carried more Neanderthal ancestry (6-9%) than any other modern human sequenced to date, owing to Neanderthal admixture within six generations before he lived. Both individuals show no genetic continuity to later Eurasian populations. Similarly, the recently sequenced female individual from Zlatý kůň, Czechia (~45,000 years or older), that appears to have contributed genetically neither to Europeans nor to Asians, carries around 3% of Neanderthal ancestry, but with segments longer than the Ust'-Ishim individual – probably an even earlier Eurasian inhabitant, following the expansion outside Africa (Prüfer et al. 2021). Differently from the Zlatý kůň and Ust 'Ishim individuals, the recently sequenced Bacho Kiro individuals (Bulgaria), dated to ca. 45-42.000 years ago (Hajdnjak et al. 2021) are closely related to present-day and ancient East Asians and American populations and had Neanderthal ancestors a few generations back.

If overall these results corroborate gene flow from Neanderthals into early modern humans expanding in Eurasia, the opposite signal (gene flow from modern humans into late Neanderthals) has not been detected so far (Lalueza-Fox 2021, but see Kuhlwilm et al. 2016 for ancient gene flow of early modern humans into the ancestors of Neanderthals from the Altai Mountains around 100,000 years ago).

These developments make it clear that recent human evolution post Out-of-Africa and interactions with Neanderthals do not comply with one single demographic dynamic, *i.e.* replacement. Other different populational processes – admixture events and possibly different dispersal waves (both of *Homo sapiens* into Eurasia and of Neanderthals across the continent, Hajdnjak et al. 2021; Vernot et al. 2021) – have contributed to shaping today's human diversity and ancestry, with different populations within the same species possibly encountering different fates.

Presently, some researchers do not theoretically rule out an "assimilation scenario" in which small, Neanderthal population pockets were absorbed into larger, expanding *Homo sapiens* groups (Bergström et al. 2021; Lalueza-Fox 2021). However, what constitutes necessary or sufficient evidence for such scenario is open to debate (Galway-Witham and Stringer 2018). What is known is that an initial, higher proportion of Neanderthal genomic ancestry, approximately 10% (Harris and Nielsen 2016), has been brought down by natural selection to present-day levels of 2%. Neanderthal DNA appears depleted around functional genomic regions and significantly in genes that are most active in the male reproductive tissue and around the X chromosome – a pattern that has been linked to reduced fertility in hybrids (Sankararaman et al. 2014).

The evidence discussed above clearly bears implications for the taxonomic status of *Homo sapiens* and Neanderthals. If Neanderthals' status has been discussed ever since it was first discovered in the 19th century, the nature of the controversy now rests on evidence of interbreeding, which has long been at best inferential among fossil data, now entering the stage as a no longer speculative line of evidence. Under the Biological Species Concept (BSC, Mayr

1942), generally inapplicable in paleontological contexts (Tattersall and Mowbray 2005) – the argument would go – distinct species status would be unjustified. In the next section we will argue that such conclusion is however over-simplistic, based on a diachronic perspective on lineage divergence and on insights provided by the evolutionary history of other animal taxa for which consistent evidence of interbreeding is available.

## 2. Species delimitation in a speciation continuum

The problem of species delimitation and of applicability of various species concepts is a notoriously hoary issue in biology, both from an ontological perspective (what species are, which we won't tackle here) and from an operational one (how we should identify species) (Hey 2001; Mallet 2013). Alternative concepts, emphasizing different biological properties, may easily come into conflict (Hey 2006; de Queiroz 2007). However, from the thriving variety of species concepts, few (Holliday 2003; Miller 2016) to none (Tattersall 1992; Tattersall and Mowbray 2005) have been said to provide a practical guide for those – palaeontologists and paleoanthropologists – who wish to recognize species in the fossil record, where morphology has long been all that the deep past had to offer. Such epistemic limitations are still predominant and relevant also in the context of very recent claims for potential new *Homo* species, as suggested (not without contention) by phenomic phylogenetic analyses of the massive cranium from Harbin, in north-eastern China (Ni et al. 2021), or for new archaic populations, like the Nesher Ramla *Homo* in Israel (Hershkovitz et al. 2021).

The context of *Homo sapiens* and Neanderthals' place in hominin phylogeny offers now a peculiar paleontological case, for which relatively generous fossil and molecular evidence are available – therefore, genetically informed operationalizations should rightfully be addressed. Nonetheless, as we shall underline, anthropologists are far from facing a unique biological case.

A growing number of evolutionary biologists now agree that species should be conceptualized as separately evolving metapopulation lineages (Wiley 1978; de Queiroz 2007), with disagreement only about where along the speciation continuum separate lineage should be considered different species. We contend that the apparent conflict now arising between paleogenomic and morphological evidence in our paleoanthropological case – a conflict that is likely to become common in the renewed discussion about species delimitation with increasing advances in knowledge and methods – should be contextualized (and thus dissolved) within a diachronic perspective on lineage divergence, where different taxonomic properties are *expected* to arise at different points in time. By saying this we are not taking a dichotomic stance with respect to the diachronic and synchronic view on species (Baum 1998; Zachos 2016). Rather, we believe that species are *both* dynamic units within processes and the results of such processes.

The formation of well-demarcated species is often a function of divergence time, whereby distantly related taxa are often easily discernible when compared. Debates, however, easily arise when it comes to discuss species status in closely related taxa, as the emergence of discrete biological entities in a continuum of change requires establishing a threshold beyond which we shall be justified in recognizing two species rather than one. A naïve approach would require such a threshold to be unique and sharply defined, *e.g.* the formation of a strong reproductive barrier. However, this approach fails to capture the temporal dimension throughout which various biological traits relevant to classification have accumulated (we could dub it the "evolutionary history load") – a perspective that is particularly relevant when attempting to establish when separately evolving lineages become species. Therefore, the absence of a particular property – even one most emphasised in literature like reproductive isolation – is not sufficient to falsify the species rank and justify a lumping move (de Queiroz 2007).

It is no wonder that many practitioners have underlined that rigorous inference of species limits should be supported by multiple and complementary operationalizations (Padial & De la Riva 2010; Schlick-Steiner et al. 2010), that provide access to the evolutionary history load and the trajectory of lineages. It has been understood that perfect congruence among criteria, although desirable, should not be considered strictly necessary, both because the process of speciation is frequently not accompanied by character change at all levels and because characters evolve at different rates during lineage divergence. A different or more sophisticated approach to integration therefore doesn't require absolute convergence but aims at identifying operationalizations and characters that can reliably track evolutionary independences, assembling various evidence cumulatively (de Queiroz 2007; Padial et al. 2010; Conix 2018). The potential of a character to be taxonomically informative should be carefully evaluated on a case-by-case basis and clearly depends on the organism at hand and on the evolutionary forces driving the speciation process. Cumulation appears to be suitable to capture more recent divergence histories (*i.e.* it does not have a bias towards older species, where congruence among operationalization is much more likely), in which the stepwise fixation of well-demarcated characters is tracked as an ongoing process.

From this perspective, we will now consider some major properties for our paleoanthropological case, which reflect major classes of contemporary species definitions. We are aware than many more are available than the ones we touch on here (Mayden 1997, Wikins 2018) but we selected the most informative and less redundant for our case (Tab. 3). These are morphological diagnosability (emphasized by phenetic and phylogenetic species concepts, Cracraft 1983; Eldredge and Cracraft 1980), the recognizability of genotypic clusters (Mallet 1995), the ecology (ecological species concept; Van Valen 1976), and reproductive isolation (biological species concept; Mayr 1942, 1963). Each of these perspectives can be prone to potential shortcomings, as it has already been largely discussed (Kimbel 1991). Simpson's evolutionary species concept (1951, 1961; see also Wiley 1978) – a general, theoretical perspective and not an operational criterion itself – bears resemblances with de Queiroz's separate evolving metapopulation lineages, so it will not be addressed as a threshold but nonetheless considered when drawing our conclusive remarks. For each property then we'll discuss if the related "threshold" has been crossed – *i.e.* if distinctiveness is appreciable based on the reference property, although our discussion won't bear implications on the exact order these properties might arise in evolutionary time. We will then briefly problematize the extent to which cultural traits should or not be included in the biological classification of species.

| **Concept** | **Definition** | **References** |
|---|---|---|
| **General lineage species concept (GLSC)** | Separately evolving metapopulation lineages (or segments therof). | De Queiroz 1998, 2007 |
| **Evolutionary species concept (EvSC)** | A phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies (Simpson 1951)<br>A lineage (an ancestral–descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies (Simpson 1961).<br>A single lineage of ancestral-descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and Fate (Wiley 1978). | Simpson 1951, 1961; Wiley 1978 |

| | | |
|---|---|---|
| **Phylogenetic species concept (PSC)** | A diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind (Eldredge and Cracraft 1980).<br>The smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (Cracraft 1983).<br>The smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts) (Nixon and Wheeler 1990). | Eldredge and Cracraft 1980; Cracraft 1983; Nixon and Wheeler 1990 |
| **Genotypic cluster concept (GSCS)** | A [morphologically or genetically] distinguishable group of individuals that has few or no intermediates when in contact with other such clusters (Mallet 1995). | Mallet 1995; Mallet 2013 |
| **Ecological species concept (EcSC)** | A lineage (or closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976). | Van Valen 1976 |
| **Biological species concept (BSC)** | A group of individuals fully fertile per se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents or sterility of hybrids, or both (Dobzhansky 1935).<br>Groups of actually or potentially interbreeding natural populations, which are | Dobzhansky 1935; Mayr 1942, 1963 |

| | | |
|---|---|---|
| | reproductively isolated from other such groups (Mayr 1942).<br>Species level is reached when the process of speciation has become irreversible, even if some of the (component)isolating mechanisms have not yet reached perfection (Mayr 1963). | |

**Tab. 3 Review of the main species concepts mentioned in this chapter.**

The table lists the main species concept that we believe are relevant for *Homo sapiens* – Neanderthal species delimitation case. The first two – the General Lineage Species Concept (GLSC) and the Evolutionary Species Concept (EvSC) – serve as primary, theoretical concepts are therefore not used as "speciation thresholds" (see Fig. 6).

### *2.1 Homo sapiens and Neanderthal biological distinctiveness*

Let us consider first the well documented morphological distinctiveness of *H. sapiens* and Neanderthals. Curiously, although different views on how to classify Neanderthals have historically alternated from the very beginning (*i.e*. Neanderthals as a wholly distinct species or a variant of *Homo sapiens*), some argue that there has never been any serious debate on whether they form a diagnosable entity (Tattersall 2007). Neanderthals are defined by a host of distinctive cranial, mandibular, dental and postcranial features, many of which are apomorphic (Kimbel 1991; Tattersall 1992). These include – although a complete survey is beyond our current scope – an ovoid ("*en bombe*") cranial profile; a lower cranial vault; rounded and double arched supra-orbital tori; a pronounced midfacial prognathism; a large nasal fossa; a receding lower jaw lacking a protruding chin; shovelled incisors; a retromolar space; a broad ribcage; robust limb bones; a wide pelvis (see table 5 in White et al. 2014 for a detailed list of characters and references). A recent analysis of a large sample of Neanderthal inner ear ossicles, which was compared with recent and extinct *Homo sapiens*, has found striking morphological differences between the two groups, although not affecting functional properties (Stoessel et al. 2016). Tattersall and Schwartz (2006) have stated that in terms of morphology alone Neanderthals constitute the most clearly demarcated extinct hominin group. The availability of sufficient individual examples has also allowed to discern a range of intraspecific variations (Tattersall 2005; Tattersall and Schwartz 2006).

There's consensus that the degree of variation among paleontological species should be equivalent to extant ones, although the choice of living model taxa is in itself contentious and even more problematic in paleontology (Kimbel and Martin 1993; Harvati et al. 2003). Harvati and colleagues (2003) compared the degree of Neanderthals' morphological differentiation from modern humans to that found within and among 12 species of extant primate taxa, including both the phylogenetically similar African apes and more ecologically analogous cercopithecines. Both phylogenetic and ecological models strongly supported a specific distinction for Neanderthals.

This has led Stringer (2012), discussing the implications of evidence of interbreeding, to emphasize that merging these closed relatives in an expanded *Homo sapiens* concept would produce a species having a range of morphological variation several times that found in humans today, or in other existing primate species. Interestingly, given that morphological distinctiveness at the specific level is expected to become more evident as divergence proceeds after the initial split, also incipient Neanderthal features have been said to be sufficient to conclude separate species status (Rak 1993). It can be reasonably speculated that for such distinctiveness to be appreciable at all stages, gene flow between the two groups must have been balanced by other evolutionary forces.

Altogether, the above evidence indicates that along their evolutionary trajectories, Neanderthals and *Homo sapiens* have crossed the "phylogenetic species" threshold (*sensu* Cracraft 1983), allowing for a clear morphological hiatus to be appreciable.

The multi-locus genotypic (or genomic) cluster concept was introduced by Mallet (1995, 2013) to accommodate the intuition that species are often distinguishable, in spite of continued gene flow in sympatry. Rapidly radiating species (such as the classic model species *Anopheles*, *Heliconius*, and Darwin's finches *Geospiza*) are known to have extraordinary levels of introgression. Yet these taxa are currently readily identified as species on morphological and genetic bases (and not because reproductive isolation *per se*, contra the BSC) as they constitute stable clusters with few intermediates between them. This indicates that not only gene flow has not reached the point where lineages fuse together (even in cases where introgression is rampant), but also that selection, mutation and drift strongly contribute to keeping lineages apart also in sympatric conditions (Mallet 2016, 2020). It should be noted that specific and subspecific levels of clustering differ under such view only by the tendency to produce intermediates at overlapping zones, and setting limit values would involve a degree or arbitrary assessment. Still, Neanderthal and *Homo sapiens* genomes fairly show a bimodal distribution (Green et al. 2010) – a reasonable consequence of the separation of the two lineages for 550,000–765,000 years after their initial split – and the idea of disruptive selection outweighing the effects of gene flow has been suggested by several studies (Harris and Nielsen 2016; Juric et al. 2016). Therefore the "genotypic cluster threshold" can be said to have been crossed by the two lineages.

From an ecological standpoint, a distinction should be drawn between the ecological contexts of *Homo sapiens* before and after the Out-of-Africa range expansion (ca. 50-60 kya). Our species has emerged around 300-200 kya in Africa and there it evolved for the great part of its evolutionary history, while the Neandearthal lineage was already established in Eurasia by 400 kya (see Galway-Witham, Cole and Stringer 2019 for a review). In Africa *Homo sapiens* had to face dramatic climatic fluctuations, which were expressed through changes in precipitations disrupting niches, resources availability, distributions of early human groups and affecting whole ecological communities (Blome 2012, Potts et al. 2018). Periods of relatively increased aridity or humidity were expressed asynchronously throughout the continent, creating alternating opportunities of foraging and migration. It has been suggested that such climatic and environmental conditions played a major role in the evolution of plastic adaptive strategies and ecological flexibility, likely bolstering dispersal success (Grove 2015).

Neanderthals, on their side, inhabited a wide niche in Eurasia, spanning from warm temperate woodlands in the Mediterranean area to the cold steppe environments of Siberia. In the Levant, compared to Upper Paleolithic *Homo sapiens*, Neanderthals appeared to have explored smaller ranges around their sites, principally situated in the rugged terrain of Mediterranean woodlands and likely due to the relative abundance of resources (Henry 2017). Although *Homo sapiens* seems to have occupied colder environments than Neanderthals, different studies have attributed cold adaptations to Neanderthals, including beneficial air-conditioning capabilities of their big, wide noses, their distinctive thorax morphology and the brown adipose tissue (reviewed in Ocobock et al. 2021, Galway-Witham, Cole and Stringer 2019). Also, studies on the effects of climate on energy expenditure have suggested that Neanderthals would have had substantially higher energy needs than anatomically modern humans in similar climates, and their costly metabolisms could have put them at risk in environments with fewer resources (Froehle and Churchill 2009). Nevertheless, to thrive in their environments and during the glacial winters of Pleistocene Europe, Neanderthals would have clearly relied on substantial cultural buffering. It is therefore difficult to disentangle the cultural dimension from the physiological and morphological aspects when investigating their ecology from a species delimitation perspective (we will return to this in a few lines).

It is likely that future research will further expand Neanderthal's adaptive range and dietary ecology, which we know today it wasn't exclusively reliant on meat, but it included also seafood and plants (Power et al. 2018; Zilhão et al. 2020). Still, different responses to climate-driven niche deterioration between *Homo sapien*s and Neanderthals can offer a reasonable proxy for their ecological distinctiveness. Melchionna and colleagues (2018) modelled the degree of habitat quality and connectivity at successive time steps. Although the degree of habitat fragmentation was initially very similar for the two species, towards the end of their existence the most suitable habitat patches for Neanderthals were small and isolated. In contrast, *Homo sapiens* has been suggested to have developed a 'generalist specialist' niche (Roberts and Stewart 2018).

It is therefore reasonable to suggest that the two lineages have reached a sensible degree of ecological distinctiveness, crossing the "ecological species" threshold.

Finally, as regards the reproductive isolation emphasized by the BSC, the evidence reviewed in section 1 could be considered sufficient to conclude that the "final test" of speciation was not passed. However, a strict interpretation of the reproductive isolation criterion is just one possibility. Coyne and Orr (2004) for instance have departed from the "hard line" BSC of "no gene flow permitted", allowing for limited gene exchange among species with their sympatric relatives. Mayr himself acknowledged that closely related species can show incomplete reproductive isolation, arguing that some hybridization is permissible between biological species so long as their distinctiveness is maintained (Mayr 1963). The interbreeding criterion is then better seen as a continuum, where the extremes – full and unconditional interbreeding on one side, systematic unsuccessful interbreeding on the other – are likely the exception and not the rule in closely related taxa (Mallet et al. 2016; Zachos and Asher 2018). Moreover, it is known that species that have evolved for a long time in allopatry (even millions of years) can still successfully interbreed, plausibly because in sympatry or parapatry strong selection against hybrids viability takes place, whereas in allopatric conditions (which has been the context of *Homo sapiens* and Neanderthals for long time) there’s no need or opportunity for direct selection for or against them (Mallet 2005; Zachos and Asher 2018).

Limited invasions of the genome are widespread. Mallet (2005) calculated that at least 25% of plant species and 10% of animal species, mostly the youngest species, are involved in hybridization and potential introgression with other species. Interestingly, it has been suggested that the evolution of a stable partial reproductive isolation could even be an adaptive optimum (Servedio and Hermisson 2020). This might suggest that conceptualizing speciation as “complete” when full reproductive isolation is reached could be a biologically misplaced expectation. Therefore, more permissive interpreters of the BSC would recognize the reproductive isolation threshold was crossed by *Homo sapiens* and Neanderthals to a biologically meaningful degree.

Overall, the evidence discussed in this section would seem to confirm that distinct species status better captures the biological distinctiveness of *Homo sapiens* and Neanderthals emerging under different perspectives (Fig. 6). We are aware that no view, if taken singularly, is sufficient and immune to potential limitations. However, under a cumulative view on integration, there is a critical amount evidence sustaining evolutionary distinctiveness of the two lineages. Simpson’s (1961) formulation of species as lineages evolving separately from others “with their own unitary evolutionary role and tendencies” could be applied in retrospection. Indeed, *Homo sapiens* and Neanderthals have largely had separated evolutionary histories, although recent hypotheses of replacement of mtDNA and Y chromosomes in Neanderthals by modern humans might reduce the temporal span of effective separateness – still not affecting diagnosability (Petr et al. 2020). After their major contact at ca. 60-50 kya, they indeed encountered different "evolutionary fates" for some 10-20 kya before Neanderthals disappearance from the fossil record at around 40kya.

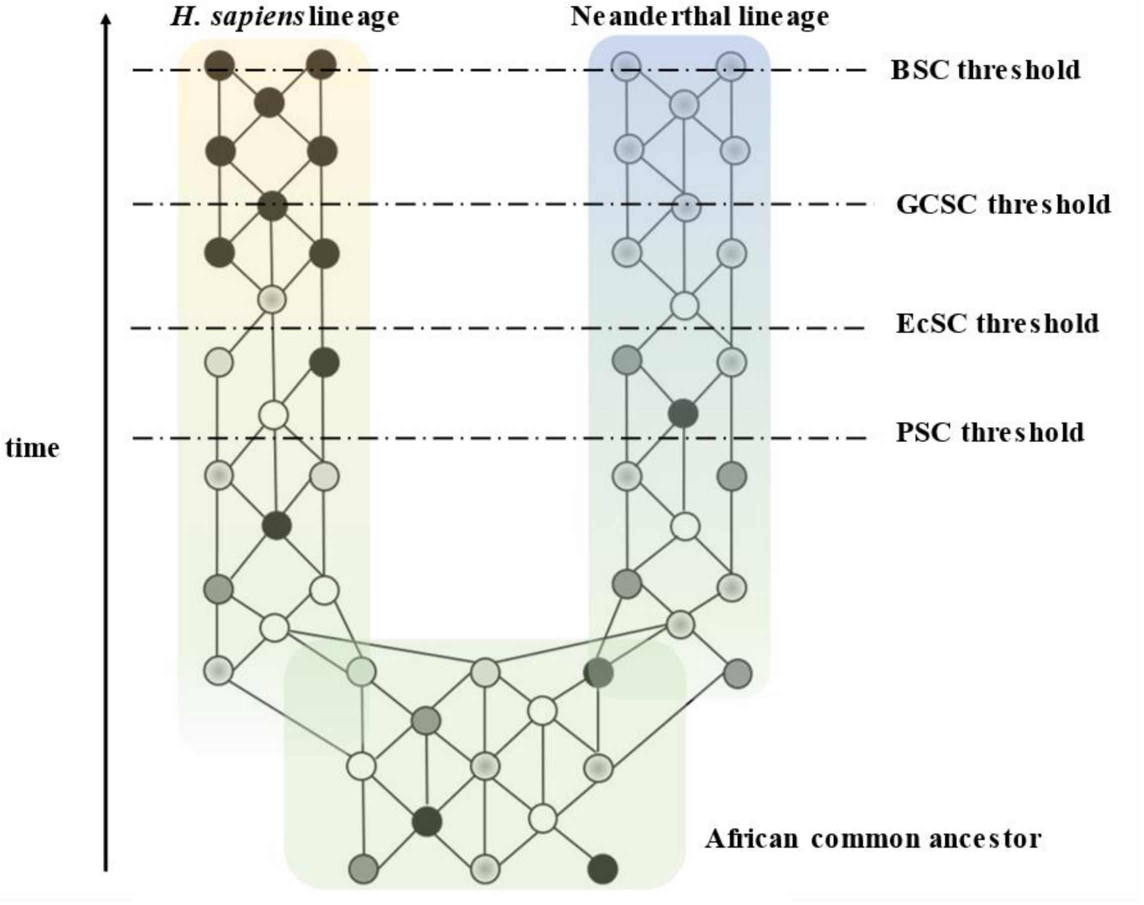

**Fig. 6 Species thresholds in *H. sapiens* – Neanderthal divergence process.**

A diachronic perspective on *H. sapiens* and Neanderthal lineages divergence, where different species concepts and the taxonomic properties they are based on are depicted as "thresholds" that are crossed at different points in time (as per de Queiroz 1998, 2007). The fixation of distinct, taxonomically relevant characters is a function of divergence time. The proposed order for the species threshold only serves as a rough indication.

A brief reflection is merited on the extent to which archaeological evidence and culture should be included in the biological classification of hominin species. From an extended, evolutionary perspective (Laland et al. 2015), it is true that the inheritance streams of biology and culture can interact to influence each other's evolution. It would be difficult then to rigidly exclude cultural evidence from biological classifications, as in some cases – such as the ecological dimension of a species – the reciprocal interdependence is evident. However, a major concern we want to raise here is that when used as *proxies* for biological distinctiveness, cultural traits can be highly misleading. *Homo sapiens* exhibits astonishing levels of within-species cultural diversity (Foley and Lahr 2011), think of a citizen of New York and a modern hunter-gatherer. It is not hard to imagine the difficulties this could pose for a future archaeologist relying on material evidence only and expecting a strong correlation between the emergence of distinctive and novel cultural behaviours and biological novelties. Moreover, cultural traits are highly dynamic entities, spreading at a higher pace than biological inheritance both within and between populations, irrespectively of their taxonomic affiliation (D'Errico and Stringer 2011). Complex cultural practices in recent hominin evolution were the outcome of complex and non-linear evolutionary trajectories, triggered by biological but also environmental, social and especially demographic factors (d'Errico and Banks 2013). There is now growing consensus that Neanderthal cultural arsenal has been underappreciated and many of the indicators of "behavioural modernity" for long uniquely associated with *Homo sapiens* are also recognized to a comparable degree in Neanderthal populations (Villa and Roebroeks 2014). Besides the reasonable difficulty of inferring makers from material traces in contexts where different hominin species were coexisting, culture might therefore be a deceptive indicator of biological specific distinctiveness, especially for recent *Homo* species increasingly relying on their learning niche (these might plausibly include also late forms of *Homo heidelbergensis*).

To conclude, if the use of the species category is a "currency" of biology and the attribution of organisms to different species taxa should follow the pragmatic goal of providing a "maximally informative ordering of nature" (Dupré 1999), we suggest that this goal, along with conveying the evolutionary history load of the two lineages, is better achieved by allowing distinct species status for *Homo sapiens* and Neanderthals (hence *Homo neanderthalensis*) than lumping them together in an expanded *Homo sapiens* taxon, despite all recent evidence for introgression.

## 3. Trees, braided streams and networks

It has been suggested that human evolutionary diversification is now best represented by a ‘braided stream” or a network (Ackermann et al. 2016; references in Stringer 2014). The extent of reticulation now evident from genomic data, under a strong version of this view, would be so great that we should abandon both specific distinctions and phylogenetic trees as outdated views. Although we are convinced that extant modern humans are not the result of diverging branching patterns only, as we have reviewed in the first section of this paper, and that gene flow has played a non-negligible role in hominin evolution, we believe that this thesis goes too far.

Here we are concerned with interactions between our own species and Neanderthals, for which different strands of evidence are available. Unsurprisingly, however, *Homo sapiens* owes up to 3.5% of its genome to another hominin group, the Denisovans, which are mostly known from DNA evidence and for which taxonomic status is still pending. Other introgressive events have been proposed for still unidentified groups – the so called “ghost populations” (to which no fossil evidence has been associated), but caution has been advanced on substantial amounts of ghost ancestry (see Bergström et al. 2021). Given our approach, we maintain our focus on the topology of Neanderthal’s and *Homo sapiens*’ lineages, but our discussion can certainly prove informative on a broader scale. We advance two main concerns to the view that we should move beyond specific distinctions and phylogenetic trees.

First, the idea that braided streams and networks should *replace* tree-like representations is built on a false dilemma. A tree topology, as it is known, is a special kind of network topology and asking which is truer is a persistent ill-formulated question, fuelling conceptual distortions. It has increasingly become clear that trees and network do not stand in opposition but co-exist, insofar as they encompass different entities and phenomena, and their usefulness as analytical tools depends on the objects of study and the questions that are being asked (Blais and Archibald 2021). As regards our case, tree-like representations and vertical phylogenies still provide a more practical and convenient tool for hominin classification, provided that they are not meant to account for all genetic relationships at play. If instead the objective is to zero in on gene exchanges within populations and across different branches, a network-like pattern would obviously better capture the desired complexity. As we have seen in the first section of this paper, the specific-level story can be broken down into different sub-histories, bringing into focus demographic complexity and different outcomes of the interactions between distinct populations. Again, each level of inquiry responds to different explanatory purposes, but care is needed in distinguishing them and their related topographies.

Second, vast portions of the tree of life topology have survived two decades of comparative genomics, even along branches where reticulation is much more pervasive, like in plant evolution. Even in such messier cases, a backbone of verticality seems to have withstood the test of time (Smith and Brown 2018; Li et al. 2019; Blais and Archibald 2021). It is therefore fundamental to consider the quantitative importance of horizontal processes: in our hominin evolutionary context, genomic evidence gathered so far have led to depiction of tree-like representations corrected with some degree of reticulation (“reticulated trees”). But this should be distinguished from unbiased networked representations, in which the distinction between vertical and lateral edges is collapsed. Branching processes still provide strong vertical scaffolds, on which occasional instances of reticulation may occur and phylogenetic conflict is still the standard to detect hybridization and gene flow.

Introgression then, now increasingly appreciated in eukaryotic evolution and known to occur most likely among closely related species, does not readily affect species tree topology and this has been assessed to be usually true for sister taxa (Mallet et al. 2016). In the progression from tokogenetic (populational-level) to phylogenetic (species-level) relationships among organisms, the degree of reticulation diminishes as hierarchical organization becomes more apparent. However, as it shall be clear by now, that divide is less sharp then previously theorized (*e.g.* one single breaking point like in Hennig's 1966 approach), as reticulation may occur across taxa which are readily identifiable to species using a variety of evidential strands (like the radiating species of model genera mentioned in the previous section). The point where the possibility of reticulation goes to zero is sensibly above the level that species classification is concerned with.

Mallet and colleagues (2016) have suggested that species are like the Ship of Theseus in philosophy, which can be almost completely rebuilt with new wood and yet remains the same ship. Our hominin case clearly remains well below the threshold where the metaphor becomes philosophically tricky (although, on a broader perspective, it might be worth reminding that besides contributions from other hominin species, our genome has a long history of borrowing gene sequences from bacteria, fungi, viruses and archaea). For invasions of the genome to derail a species from its distinctive evolutionary trajectory and confound its accumulated evolutionary history load, these must be in a significant amount and interact considerably with evolutionary processes at the specific, biological level.

As for *Homo sapiens* and *Homo neanderthalensis*, as we have argued throughout this paper, we ultimately believe that this point has not been reached yet, and therefore suggest paleogeneticists to abandon the use of ambiguous wording as ‘intermixing populations’ or ‘archaic groups’ in favour of a more congruent use of the word “species”, as in use in zoological nomenclature.

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# 5.

# Human niche construction and the climate crisis

## Anthropogenic climate change as a monumental niche construction process: background and philosophical aspects

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### Abstract

Climate change has historically been an evolutionary determinant for our species, affecting both hominin evolutionary innovations and extinction rates, and the early waves of migration and expansion outside Africa. Today *Homo sapiens* has turned itself into a major geological force, able to cause a biodiversity crisis comparable to previous mass extinction events, shaping the Earth surface and impacting biogeochemical cycles and the climate at a global level. We argue that anthropogenically-driven climate change must be understood in terms of a monumental *niche construction* process, generating long-term ecological inheritance and eco-evolutionary feedbacks that are putting our health and well-being and those of future generations at risk. We then list five major sources of climate change counter-intuitiveness, highlighting how evolved cognitive biases and heuristics may stand in the way of providing effective responses within tight deadlines. Drawing on our framing of the climate breakdown, we finally call for an evolutionary perspective in approaching the adaptive challenge posed by climate change: we argue that putting the brakes on a genuine self-endangering evolutionary trap ultimately depends on our counteractive niche constructing abilities, played at the level of our institutional and innovation capacity.

## Keywords

Anthropocene; climate change; cognitive bias; human evolution; niche construction; sixth mass extinction

## 1. Human evolution and climate change

An increasing amount of evidence is showing today how our evolutionary history has been strongly connected to the drastic fluctuations that characterized past climate on Earth (Potts 2012, 2013; Maslin et al. 2014; Grove 2014; Owen et al. 2018). The Pleistocene, the geological epoch spanning between 2.5 million years ago and 11,700 years ago, is known as a period of great climatic instability, during which a series of glacial and interglacial climatic cycles occurred, with swings between moist and dry phases. More specifically, fundamental shifts in African climate have been identified near 2.8 Mya, 1.8 Mya and 1.0 Mya, datings that today draw on a new set of fossil and paleoclimatic data and that correspond to key junctures in early hominin evolution, including the emergence of genus *Homo* (de Menocal 1995; National Research Council 2010; Schultz and Maslin 2013; Maslin 2017).

Early humans evolved to live with a high degree of uncertainty and had to face tough adaptive challenges, being soon able to survive in environments that were nothing like the African cradle of humankind. Some scholars have been studying past climate change in association with some of the defining characteristics of our species, like bigger brains and complex tool use, suggesting that climate change has played a role in triggering evolutionary advances and in determining the extinction and the origin of hominin species. The "variability selection hypothesis" (Potts 1998) has been proposed in contrast to the "habitat-specific hypothesis", arguing that environmental instability rather than single types of habitat (like open grasslands) or directional trends shaped key events in human evolution (Potts 2012, 2013; Grove 2011).

Early bipedalism, highly encephalized brains and complex human sociality are understood by this hypothesis as a sequence of variability selection adaptations, meaning that responsiveness and versatility have been ratcheted up to cope with novel and rapidly changing environments. This draws attention to the fact that the presence of genus *Homo* in early fossil records is not restricted to a single type of habitat. A striking example of the high degree of tolerance of different environments is the dispersal of early *Homo (Homo ergaster),* starting from 2Mya, beyond African territories into European and Asian environments (Antón 2003). In Asia, a new variant would have emerged (*Homo erectus*) – a highly variable species, covering disparate geographic areas, from Java to China, also found in locations relatively far north (Rightmire 2001).

Migration phenomena in our evolutionary past alone demonstrate how climate change has always been a major evolutionary determinant for us. Besides the above-described expansions (collectively known with the informal term "Out of Africa I"), a second Out of Africa took place between 800 and 650kya, with *Homo heidelbergensis* expanding in Asia and Europe (Rightmire 1998; Manzi 2011), and a third one, possibly beginning before 200.000 years and with a more significant recent wave between 50 and 70.000 years ago (Harvati et al. 2019, Rito et al. 2019) would have led *Homo sapiens*, through different waves of peopling at different latitudes and with unprecedented rapidity, to become a global species. We evolved to live with change, and many of the features that make us human are the result of our migratory past (Parravicini and Pievani 2016).

But climate change, of course, cannot be interpreted as a driver of evolutionary innovation only. When faced with strong and sudden environmental changes, a species (ours included) has three options: respond to the increased unpredictability of the environment with greater behavioural flexibility that may enhance its survival and genetic contribution; migrate sufficiently rapidly to more suitable habitats, or die out. Therefore, climate variability, when exceeding degrees of tolerability, can also be the major cause of extinction of species that have proved successful for a long time.

The questions now is to what extent *Homo sapiens*, the species that has survived among the diversity of so many hominin species, will succeed in limiting the magnitude and the temporal persistence of the profound alterations caused to its own environment (affecting the composition of the atmosphere, the marine biogeochemical cycles, the sea levels, etc.) – changes that can even continue to exert their impact for the next ten millennia (Solomon et al. 2011; Hönisch et al. 2012; Clark et al. 2016). The one that is unfolding before our eyes is a high-risk evolutionary experiment, in which one species will have no choice but to produce an adaptive response to the environmental changes that have been triggered by its own activities. The available window for action to mitigate climate change, in order to prevent the deleterious impacts from growing and involving an increasing number of generations after ours, is closing rapidly.

The purpose of this paper is to highlight the importance of integrating an evolutionary perspective to fully understand the deep-rooted causes and the long-term consequences of the climatic crisis. After having briefly introduced the relationship between climatic factors and key events in our evolutionary history, in the following section we will substantiate the role of *Homo sapiens* in today's extinction crisis and the contribution of climate change in bringing forth specific macro-evolutionary patterns (most notably, mass-extinctions).

In what follows, we will make a case for *Homo sapiens'* transformative capacity in reconfiguring biodiversity and the climate system as an instance of a complex niche construction behaviour (Odling-Smee et al. 2003; Kendal et al. 2011) that has deep historical roots, underlining in particular how the transformation of the selective pressures is generating evolutionary feedbacks and feed-forwards on us constructors, turning our niche construction abilities into potentially maladaptive behaviours. Then, the climate crisis poses a problem that must be read also in evolutionary terms for the consequences it entails; similarly, of evolutionary origin are also the cognitive biases (once likely adaptive) that prevent us from taking effective action: behind today's greatest global challenge, an evolutionary short circuit stands out.

## 2. The contribution of climate change to the current extinction crisis

It is still debated whether the informal term "Anthropocene"– first introduced by the atmospheric chemist Paul Crutzen and the ecologist Eugene Stoermer (Crutzen and Stoermer 2000) to identify an epoch characterized by the footprint of human activity– should be considered as a new chronostratigraphic unit (Rull 2018) and, if so, where its historical beginning should be placed (Ruddiman et al. 2016; Zalasiewicz et al. 2017; Ruddiman 2018, Zalasiewicz et al. 2019). The committee of 34 researchers forming the Anthropocene Working Group (AWG) is currently working on identifying a suitable global boundary stratotype section and point (GSSP), or 'golden spike' – a geological marker that recurs globally and will be part of the sediments of future geological record (Waters et al. 2018). The formal proposal that the AWG will submit by 2021 to the International Commission on Stratigraphy (ICS) will probably choose the radionuclides that came from atomic bomb detonations of the mid-twentieth century as a signal that can be found globally in the geological record (Waters et al. 2015; Zalasiewicz et al. 2019)

Other scholars instead call for a more gradual and deeper time perspective in understanding human transformative power of Earth-systems (Boivin et al. 2016; Ellis et al. 2016; Ruddiman 2018 – among these, Ruddiman argues against *any* formal definition of the Anthropocene). Boivin et al. (2016) in particular identify four major key-phases that provide examples of wide-reaching anthropogenic changes (based on decades of archaeological, paleoecological and genetic research and records): the Late Pleistocene dispersal of *Homo sapiens*; the emergence and spread of agriculture (early Holocene); the colonization of world's islands; the emergence of centralized human settlements and trade (Bronze Age). Without downplaying the role played by recent industrial economies and by the Great Acceleration (Steffen et al. 2015), a gradualist perspective in assessing broad anthropogenic impact is certainly suitable here, if we want archaeological and paleoecological data to weigh in and to highlight the far-reaching consequences of processes that have been in play for a long time. The onset of agriculture itself, whose first instances emerged at different places and at different times, cannot be captured through a "saltationist perspective" of an abrupt single start (Ellis et al. 2016, Stephens et al. 2019).

Concerns have been raised also on the identity of the “*anthropos”* component in the Anthropocene term, *i.e.* whether humanity in general as the “human enterprise” should be held responsible for causing massive ecological disruption or, instead, some specific human groups (Hartley 2016), as well as on the utility of the formalization of the Anthropocene in motivating political action (see for instance Santana 2019).

Regardless of whether the term will receive formal scientific ratification or not, it is now hardly disputable that human activities on the planet reached the same scale or have even exceeded natural forces in altering different aspects of the planet at a global level (Steffen et al 2004, Ruddiman 2018). Very few (if any) scientists would question now that *Homo sapiens* has become the dominant evolutionary forces of his era (Palumbi 2001), being fairly comparable, as regards to the speed of impact and the mortality rate, to the previous “Big Five” catastrophes of the past 540 million years (Barnosky et al.  2011), caused by volcanic eruptions, ocean acidification, climatic fluctuations, changes in atmosphere composition, impacts of asteroids on Earth, or a combination of these factors. The expression “sixth mass extinction” (Leakey & Lewin 1992) can no longer be reduced to a catastrophic metaphor.

Many scholars (Barnosky et al. 2011; Dirzo et al. 2014; Ceballos et al. 2015; Ceballos, Ehrlich, Dirzo 2017) have highlighted the dimensions of the current extinction crisis – the numbers of which tend to be underestimated, since the majority of species have not yet been formally described – by comparing fossil and modern data, documenting both rates and magnitude of extinctions. Barnosky et al. (2011) assess that “current extinction rates for mammals, amphibians, birds and reptiles, if calculated over the last 500 years, are faster than (birds, mammals, amphibians, which have 100% of species assessed) or as fast as (reptiles, uncertain because only 19% of species are assessed) all rates that would have produced the Big Five extinctions over hundreds of thousands or millions of years”. The conclusion of the study is that the recent loss of species “does not yet qualify as a mass extinction in the paleontological sense of the Big Five”, but still we’re underway to reach that dramatic threshold in just a few centuries, if the stressors and the feedbacks among them are not mitigated.

Dirzo et al. (2014) proposed the expression “Anthropocene defaunation” to describe the pervasiveness of the anthropogenic impact on terrestrial fauna. Every year we are likely losing a total amount of 11,000 to 58,000 species, concentrated mainly in tropical regions, and since 1500 at least 322 vertebrate species have become extinct. A less known phenomenon, the contraction of biodiversity in invertebrates, seems to be as severe as the vertebrate defaunation: 67% of monitored populations show 45% mean abundance decline (Dirzo et al. 2014). As shown by the recent report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, nature across most of the globe has now been significantly altered by multiple human drivers, with the great majority of indicators of ecosystems and biodiversity showing rapid decline, and human actions threaten more species with global extinction now than ever before (IPBES 2019). The IPCC Special report on 1.5° of global warming highlighted recent findings that the inertia in responses of some species to climate change may lead to unknown implications for biodiversity and ecosystem function (IPCC 2018), whereas climate change is yet a direct driver that is increasingly exacerbating the impact of other drivers on nature and human well-being (IPBES 2019).

In fact, as regards the factors causing mass-extinction phenomena, climate change is certainly a major contributing one. According to a “perfect storm” model of mass extinctions – one that identifies multiple convergent factors rather than a single cause to explain macroevolutionary patterns – three are the major conditions that simultaneously can bring forth a mass-extinction as a consequence (Arens and West 2008; Brook et al. 2008): i) accelerated climate change; ii) alterations of atmosphere composition; iii) ecological stresses with abnormal intensity.

The convergences of these three conditions, as well as positive feedbacks among them that could further increase the severity of the consequences, are common features of the “Big Five”, and have resulted in mass extinctions in the past, but it’s easy to see how the current situation perfectly fits the schema (Barnosky et al. 2011). In fact *we do* have accelerated climate dynamics (i), rapidly approaching the different tipping points existing for different large-scale components of the Earth system (critical thresholds at which a tiny perturbation can qualitatively alter the state or development of a system) (Lenton et al. 2008; Rockström et al. 2009), *i.e.* Arctic sea-ice, Greenland or West Antarctic ice sheet, Atlantic thermohaline circulation, El Niño–Southern oscillation, Indian or West African monsoons, amazon or boreal rainforest. According to an updated and extended analysis of the Planetary Boundaries concept – those boundaries that define the safe operating space for human activities with respect to the Earth’s biophysical subsystems and processes (Rockström et al. 2009) – four of nine of them have now been crossed: climate change, loss of biosphere integrity, land system change, altered biogeochemical cycles (Steffen et al. 2015). *We do* witness alterations of atmospheric composition (ii), as $CO_2$ levels continue to rise and have reached levels unprecedented for at least the last two million years (IPCC 2013). And *we do* have ecological stressors of unparalleled intensity (iii), acting at an increased pace since the beginning of the industrial era (Abram et al. 2016). The feedbacks among individual stressors have already been triggered, but we’re still in an early phase of this.

## 3. Climate change as global niche construction at work

In evolutionary terms, the transformative changes at a global scale produced by the representatives of our species can be fruitfully understood as a *global niche construction* process (Odling-Smee et al. 2003; Kendal et al. 2011; Boivin et al. 2016; Laland et al. 2016).

The critical alteration of the climate due to anthropic activities is perhaps the greatest example of monumental niche modification produced by one species alone.

Niche construction (henceforth NC) is defined as the process by which organisms actively modify, in nonrandom ways, their own and each other's evolutionary niches (Odling-Smee et al. 2003), and their legacy over time (ecological inheritance). Typical examples of NC in other animals include the building of nests, burrows and dams (beavers) and the alteration of physical and chemical conditions of the soil (as in the case of earthworm soil processing). NC may occur with the organism proactively initiating a change in its selective environment (inceptive NC) or responding directly to prior changes (counteractive NC); such changes may be perturbative with respect to the environment or imply a relocation of the organism into novel habitats (Odling-Smee et al. 2003, Table 2.1).

Clearly, *Homo sapiens'* complex NC behaviour cannot be reduced to the counteractive nor the relocation kind, especially as regards its recent evolutionary past, where signs of increasingly perturbative and inceptive activities are everywhere. It differs markedly from other species NC not just in the scope of environmental alterations, but also in what triggers those alterations. Some scholars suggest that humans are better described now as "niche modifiers" (Low et al. 2019), since their cumulative and progressive activities today are not necessarily driven by an adaptive need or pressure: they are largely determined by cultural rather than biological factors (like the individual and collective ambition towards an increasingly comfortable life). Indeed, the reason why human niche has become predominant on the biosphere is strictly connected to the fact that we have unrivalled capacities for learning: if the deliberate alterations we impose are driven by our socially transmitted information, culture and shared conventions (Laland and O'Brien 2012), these can be passed both within and across generation, thus spreading and evolving far more rapidly than any other biologically determined trait. As seen in the previous section, this capacity for advanced cognition and complex NC activities is not a modern phenomenon but has been exercised and enhanced for thousands of years of evolution, culminating in almost irreversible changes to planetary ecosystems. Our fast-evolving sociocultural niche (Ellis 2016) then can easily lock us into long-term cycles of adaptation if the alterations we impose have an evolutionary significance. In fact, NC theory proponents argue that environmental modification and subsequent ecological inheritance are to be understood as *evolutionary processes*, which means that constructor organisms, by modifying environmental states in non-random ways, impose a systematic bias on the selective pressures they produce, generating networks of causation that can feedback on themselves (Matthews et al. 2014; Laland 2014).

Matthews et al. (2014) have identified three criteria to test for the presence of niche construction (Criteria 1 and 2) and to determine when it affects evolution (Criterion 3):

1. an organism must significantly modify environmental conditions;
2. organism-mediated environmental modifications must influence selection pressures on a recipient organism;
3. there must be an evolutionary response in at least one recipient population caused by the environmental modification.

We argue that these criteria are perfectly met by the role played by *Homo sapiens* in the climate crisis: therefore, a non-trivial application of the NC perspective can be particularly useful here to highlight undervalued evolutionary implications and risks of anthropogenic climate change. The first criterion is already convincingly satisfied: in the last million years anthropogenic climate change has been the most dramatic expression of environmental alteration due to activities of an organism. Human activities have caused approximately 1.0°C of global warming above pre-industrial levels (IPCC 2018) and information from paleoclimatic archives shows that the pace and extent of the variations of many other components of the climate system (*i.e.* sea ice) are unprecedented in the context of the past centuries (Masson-Delmotte et al. 2013). Among the already known associated impacts are to mention sea level rise, changes in land and ocean ecosystems and services, retreat of glaciers, sea ice and ice sheets, biodiversity loss and related risks, such as the spread of invasive species and forest fires.

Warming from anthropogenic emissions and activities has caused a vast array of long-term changes in global ecosystems, both on land and into the oceans. As stated by the IPCC Special report on 1,5°C of global warming (Hoegh-Guldberg et al., 2018), the $CO_2$ release (mainly from fossil fuel combustion) has already determined a shift in ocean pH that with high confidence is unprecedented in the last 65 Ma of Earth's history. According to Hönisch et al. (2012), this alteration of ocean acidity stands out as capable of driving a combination and magnitude of ocean geochemical changes potentially unparalleled in at least the last ~300 My of Earth history, raising the possibility that we are entering an unknown territory of marine ecosystem change.

Besides this, a commonly neglected aspect of climate change is the fact that its consequences are entering a dangerous evolutionary game, altering the selective pressures acting on different organisms (criterion 2). For example, changes in seasonal timing of the major life-history events and other phenological responses are already documented effects of climate change, with disruptions to the timing of migration and breeding, and asynchronies and loss of connectedness among interacting species (Cohen et al. 2018; Root et al. 2003). Leaf unfolding, flowering, the foraging activity of pollinators and avian migration are just a few of the phenomena for which phenological mismatches have been reported in the scientific literature (Dirzo et al. 2014; Rafferty 2017).

Organisms, when facing a changing environment, must find some adaptive means to respond to the new situation, whether by phenotypic plasticity, migration to a new location with similar conditions, or by genetic change (criterion 3). But where the rates of environmental change are too fast to maintain adaptedness, widespread maladaptations and extinctions are expected (Merilä et al. 2016). In particular, we want to draw attention to the fact that by affecting complex eco-evolutionary dynamics we're creating all the premises for an evolutionary trap for ourselves too (Schlaepfer 2002). With this regard, what are the eco-evolutionary feedbacks of *sapiens*-induced climate change acting on us? We're integral part of the ecological niches we've altered and our very existence depends on the ecosystem services that healthy natural environments can provide (Cardinale et al. 2012), so we must expect that the globally altered selective pressures are also affecting our own life-supporting conditions, our health and our future evolutionary history.

It has recently been demonstrated that, under a business-as-usual scenario, the geographic position of the narrow temperature niche in which humanity has flourished for millennia will shift more over the coming 50 years than it has moved over the past 6000 years, leaving 1 to 3 billion people outside the favourable part of the climatic envelope and mostly affecting the regions with the lowest adaptive capacity (Xu et al. 2020).

Among the many threats that climate change has posed to our civilization, an alarming one is the spread of infectious diseases, exacerbating health problems in vulnerable populations and acting as a brake in socio-economic development. The transmission of vector-borne diseases, that account for more than 17% of all infectious diseases (WHO 2017), is known to be vulnerable to temperature and rainfall trends (Shuman 2010). Current predictions of climate change show an increase in mosquitoes such as *Aedes aegypti* and *Aedes albopictus*, both as regards distribution and the ability to transmit diseases such as dengue, Zika, and yellow fever (Kraemer et al. 2015).

Food availability and security is another important aspect that is highly impacted by climate change. Climate variability and change will worsen food insecurity in areas already affected by hunger and undernutrition (Wheeler and von Braun 2013). Recent projections (that are still under debate due to the alleged linearity of the involved processes) indicate that each degree-Celsius increase in global mean temperature could, on average, reduce global yields of wheat by 6.0%, rice by 3.2%, maize by 7.4%, and soybean by 3.1% (Zhao et al. 2017).

Moreover, as in our evolutionary past, we are witnessing today an increasing trend in environmental migrations. The 2018 Global Report on Internal Displacement shows that in 2017 a total of 18.780.000 people have been displaced by disasters, more than 8 million and a half coming from East Asia and the Pacific regions (IDMC 2018). Within-country data are more generous compared to across borders data, but research is being improved in these years.

Impacts related to climate change affect our society on different levels and in many sectors on which our health and wellbeing depend. What we are facing is a genuine evolutionary challenge, to which first of all adaptive measures - mostly played at the level of our cultural and social evolution - must be offered within tight deadlines. Cultural, political and technological strategies are needed to ensure the survival of the natural ecosystems than can still be rescued (some of these, like coral reef ecosystems, have already been strongly compromised), with the awareness that these very same ecosystems, in turn, guarantee the life-supporting conditions for current and future human societies. Systems transitions, unprecedented in terms of scale, are also required to limit the magnitude of global warming (IPCC 2018).

As typical of any recursive interaction, like the constructor organism-environment interplay in NC processes, we are the driver of change, but this does not imply that the whole process is under our control. We *Homo sapiens*, experienced niche constructors and major evolutionary drivers of the ongoing sixth mass-extinction, are now threatening the survival of our own civilization.

## 4. The ecological inheritance of climate change

Abatement of greenhouse gas emissions ("mitigation", IPCC 2014a) are no longer enough to avoid the effects that have already been triggered on the environment and on human societies. We must adapt our lives, behaviours, cities, societies to the outcomes of climate change already in the pipeline *i.e.* we have to produce now an adaptive response to the outcomes of our prior choices ("adaptation", IPCC 2014b). This reciprocal causation (Laland et al. 2011, 2013) is a hallmark of ongoing niche construction processes: as seen in the first section, environment and climate have strongly influenced our evolution as a species; on our part, we have dramatically altered the state of those very same environmental drivers in such a way that we are now forced to counteract them adaptively, mostly through major cultural responses, to avoid social collapse. It is clear that with climate change impacts speeding up (i.e. Greenland and Antarctic ice sheets are melting much more faster than in the last centuries, Meredith et al., 2019) – the longer we wait, the more dramatic our actions will need to be (and the higher the economic costs).

All these aspects evidence once again the evolutionary scale reached by the climate crisis today. NC perspective allows us to highlight another fundamental evolutionary implication, *i.e*. the legacy of current climate breakdown. Through ecological inheritance – a system of inheritance that is generated whenever the environmental consequences of prior niche-constructing activities persist or accumulate as modified natural selection pressures (Odling-Smee 2010) – we have committed ourselves and our descendants to a physical, biological and social world that is qualitatively different from the one that gave rise to *Homo sapiens* and its cultural evolution. Under an expanded concept of inheritance, that of *niche inheritance*, parent-offspring similarity depends then on two transmission channels: the genetic (associated with biological reproduction) and the ecological one (transmitted through the external environment).

In the case of human evolution, ecological inheritance also includes the transmission of semantic information in the form of "cultural knowledge" through social learning (human ecological inheritance then involves both principal kinds of heritable resources, energy and matter and semantic information, Odling-Smee 2007; Odling-Smee and Laland 2011). Undoubtedly, technological innovations and social learning have played a major role in helping humans transforming and settling in harsh habitats for which they were poorly suited biologically (sociocultural NC, Boyd et al. 2011, Ellis 2016). Moreover, unlike genetic inheritance, where genes in sexual populations are transmitted by two parents at a time, ecological inheritance (and with it cultural inheritance) is relentlessly transmitted by multiple individuals to multiple other individuals, both within and between generations. Ecological inheritance doesn't need to involve genetic relatives: it can be transmitted by other non-related individuals in shared ecosystems, at a much faster rate than the transmission of any biological trait.

With this in mind, it is worth remembering that there's solid evidence that the changes we have produced (those that have already occurred and those "in the pipeline") in global temperature, atmospheric and ocean chemistry and average sea levels will last for many centuries, a long-term commitment then not just for this century, but for the next ten millennia and beyond. The estimate from Clark et al. (2016) is worth quoting at length: "(…) the twentieth and twenty-first centuries, a period during which the overwhelming majority of human-caused carbon emissions are likely to occur, need to be placed into a long-term context that includes the past 20 millennia, when the last Ice Age ended and human civilization developed, and the next ten millennia, over which time the projected impacts of anthropogenic climate change will grow and persist". As intentional niche constructors and deliberate actors of a non-linear transition, we have already impacted future generations that, despite not being part of today's decision-making processes, will ecologically inherit most of the subsequent consequences.

Yet, in spite of all evidence and scientific consensus on the far-reaching consequences of the climate crisis, the international efforts in dealing with such global, self-produced ecological changes have been so far very limited in scope. A further dimension of the problem, that will be discussed in the next sections, resides in the deeply-rooted cognitive challenges that stand against our chances of grasping the dimensions and dealing effectively with climate change. These, we will argue, have been important elements of our sociocultural NC, likely bearing once an adaptive value: now, if not adequately addressed, they could trap us into a self-endangering maladaptive behaviour.

From the signing of the robust United Nations Framework Convention on Climate Change (UNFCCC) in 1992 and of the insufficient Kyoto Protocol in 1997, the international negotiation on climate change has moved to the bottom-up approach of the Paris Agreement (sealed in 2015), based on voluntary and transparent commitments of the adherent nations. Although many have observed the potential of the "pledge and review" structure of the Agreement (Jacquet and Jamieson 2016; Averchenkova and Bassi 2016), the global emissions outcome of the submitted mitigation ambitions would lead, within the current century, to an increase in mean temperatures around 3,2 degrees (UNEP 2018), with all the panoply of well-known consequences.

With the existing emission mitigation policies, we have only a 5% chance of keeping global temperature increase under 2 degrees by 2100 (Raftery et al. 2017). In order to fall even within this 5% chance, radical and immediate actions would be needed for a faster global decline in carbon emissions. To limit global temperature increase "well below 2°C" of pre-industrial levels (let alone to pursue all efforts to stay below +1.5°C) the speed of decarbonisation should be dramatically increased, deforestation should be stopped and also a huge amount of carbon will need to be removed from the atmosphere (Rockström et al. 2017). Huge inconsistencies still exist between science-based targets and national commitments.

Despite thousands of non-State actions have been formally declared by cities, regions, companies, investors, civil society organizations (UNFCCC-NAZCA 2019), and despite the increased public concern about the climate crisis (as testified by the massive "Climatestrikes" in 2019), the assessment of actions by the G20 countries indicates that this drastic change is yet to happen; in fact, global $CO_2$ emissions increased in 2017 after three years of stagnation (UNEP 2018).

Leaving aside the social, economic and geopolitical aspects, we believe that the reasons for the failure so far in figuring out effective solutions include an evolutionary explanation. Throughout our evolutionary history, as previously stated in this paper, we have strongly relied on learning abilities to ensure our survival and well-being in our sociocultural niches: as a result, some cognitive mechanisms that bias our reasoning have become hardwired. We want now to expand our evolutionary approach in taking a closer look at those constraints that have evolved with us: it is only through a deep-history perspective (as we've provided so far) that far-sightedness in action can be achieved.

## 5. The deeply-rooted cognitive challenges of climate change

Different scholars have called for a cognitive science perspective in understanding why people fail to grasp human-environmental relationships accurately and to take the environmental crisis seriously (Amel et al 2017;  Johnson and Levin 2009; Sörqvist and Langeborg 2019; Spence et al. 2012; Weber 2017).

Indeed, decades of research on judgment and decision-making have already established that a number of biases and shortcuts (simplifying heuristics) may disrupt rational discourse and prevent people from making fully-rational choices when facing complex problems (Tversky and Kahneman 1974; Gilovich et al 2002). These may be effective in conditions with specific time-constraints and lack or overload of relevant information. Analogous deviations from economically rational expectations seem to be also shared by other organisms: honey bees seem to behave pessimistically when agitated and domestic dogs show negative contrast effects (Fawcett et al 2013), so our biases may appear to have deep evolutionary roots.

Under an ecological perspective on cognitive biases (Gigerenzer and Gaissmaier 2010) it is reasonable to think that perceptions, reactions and decision rules have evolved to perform well in presence of statistical properties of the environment – commonly encountered ecological contexts during the individual's evolutionary history (see also Fawcett et al 2014). The complex niche we have moulded is not a place of immediate threats, time-constrained risks, short-term and locally visible changes, straightforward cause-effect relationships. Climate change is a cognitively demanding object, an "hyper-object" (Morton 2018) that cannot be completely grasped through local manifestations: in evolutionary terms, the associated problems it poses and the impact on our behaviour are somehow novel for our heuristics, that may be largely useful in solving problems on which they have long been trained; however, when faced with a complex array of interdependent variables and statistical trends, misperceptions can easily arise.

Drawing on available literature and our own framing of the climate crisis, we shortlist below five main unprecedented challenges posed by climate change, that represent major barriers to our evolved cognitive processing capacity, thus undermining the chances of abandoning current status-quo. Each challenge must be interpreted as a source of counterintuitiveness with respect to our ability to grasp the meaning of what is happening with climate change.

1. First of all, climate change is not a single phenomenon, but a cluster of physical, environmental, social and economic changes: climate change is a *multidimensional* problem and a complex system (that extends to global governance, market failures, technological research, global justice, and the circular causation among them). As typical of any complex system (the notion of complexity itself arose in concert with atmospheric processes - see Rind 1999 for a viewpoint on complexity and climate), multiple cross-scale interactions take place between many different components. Clearly, causal links in such a nonlinear and dynamic system can be tricky and lead to counterintuitive perception: colder winters could be a counterintuitive effect of climate change and the global warming trend (see Kim et al 2017 for a link between warmer Arctic temperatures and colder North American winters). This and analogous conclusions are examples of "end point bias" that can lead to here-and-now weakening of the consensus on a long-term temperature trend (Hardy and Jamieson 2016).

2. Climate change, in terms of human generation rates, is still a slowly evolving process that can elude individual perception and tends to be quickly normalized. This is a problematic feature for our collective awareness. The risk of normalizing the conditions of steadily worsening environments has been observed also in other fields, especially as regards biodiversity decline and ecosystem health, where this phenomenon is referred to as the "shifting baseline syndrome" (Pauly 1995). Moore et al. (2019) have provided evidence for an analogous effect with respect to human experience of climate change. This has potential implications for both the acceptance of climate change and public pressure for mitigation policies. We're at risk of normalizing extreme weather events when we should be more worried about them. We tend to evaluate meteorological weather as either normal or abnormal based on short-reference periods, like personal

memory and experience and individual lifetime, failing to grasp the risks associated with a long-term and global phenomenon (Sharpe 2019).

3. Climate change develops on a global scale both temporally and geographically, and its effects are unbounded in time and space. We intuitively tend to focus on recent and local data ("cognitive myopia", Weber 2017), while the damages of our climate-changing behaviors often extend to people very far from us in space (mostly in developing countries in tropical and equatorial bands, IPCC 2014b) and in time, i.e. the next generations (Clark et al. 2016). A millennial timescale is very abstract for immediate intuition and minds not scientifically trained. This temporal and geographical "dispersal" of causes and effects of climate change (Gardiner 2011, Jamieson 2014) may have significant consequences, like blurring ethical commitments towards spatially distant people or future generations, or even fostering denial (to evade uncomfortable realities or preserve identity-defining commitments, Cohen 2001; Kahan et al. 2012).

4. Climate change requires actions whose effects will be perceived, if all goes well, by future generations. Concrete action can be seen as expensive in the short-run, but these investments will prove to be beneficial in a long-term perspective. This form of "hyperbolic discounting" (Laibson 1997, IPCC 2014a), leads intuitive thinking to discount future costs or benefits at a non-constant rate ("hyperbolically"), so that an immediate but smaller benefit tends to be preferred over a larger but later reward. In many cases, climate change mitigation responses are delayed due to a focus on the upfront costs of many measures, whereas future benefits of those investments are weighted less. Although a short-term focus may have been helpful to ensure immediate survival during human evolution, a lack of vision could invalidate possibilities of action

in complex niches, where risks are not visible locally and have no short-time horizons (resulting in the incapability of perceiving climate change as an immediate threat worth of immediate action, Swim et al. 2009).

5. Finally, climate change is a probabilistic and statistical affair. This means that specific events will likely happen under specific conditions, and within an assessed time frame. The scientific consensus is very robust about the causes and the general trends in progress that await us in the short and medium term (Cook et al. 2016, IPCC 2018) (increased global average surface temperature, changes in precipitation rates, accelerating ice melt, global mean sea level rise, ocean acidification, increased risk of extreme weather events, increased wildfire incidence, exacerbation of the ongoing sixth mass extinction), but the regional and local trajectories and events can be influenced by a set of contingent factors, on a case-by-case basis, see connections with point 1). The IPCC reports are known to employ a calibrated language to express the level of confidence associated with each key-finding (using main five qualifiers: very low, low, medium, high and very high; the following terms are used to assess the likelihood of a result: virtually certain 99–100% probability, very likely 90–100%, likely 66–100%, about as likely as not 33–66%, unlikely 0–33%, very unlikely 0–10%, exceptionally unlikely 0–1%) (cfr. IPCC 2018, p. 6). Research on the interpretation of IPCC verbal probabilities has shown that people tend to assign numerical probabilities that deviate substantially from those of the IPCC guidelines (Budescu et al. 2014). Climate change urges us to feel responsible for the probability (not the full certainty) of the outcomes of our choices. But probabilistic thinking and statistical judgement have been proved to be highly counterintuitive for *Homo sapiens*' brain and are thus prone to frequent errors (Kahneman and Tversky 1982; Kahneman 2011).

Summing up, the above-listed features are concrete barriers to forward-looking decisions on which the long-term wellbeing and survival of our civilization strictly depend. There seems to be an evolutionary short circuit with no apparent way out: we've produced global-scale changes with self-defeating consequences over the next millennia because of our evolved niche-constructing abilities; concurrently, what prevents us from taking action are the limitations of our evolved processing capacity. As Jamieson pointed out, "evolution built us to respond to rapid movements of middle-sized objects, not to the slow build-up of insensible gases in the atmosphere. Most of us respond dramatically to what we sense, not to what we think. As a result, even those of us who are concerned about climate change find it difficult to feel its urgency and to act decisively" (Jamieson 2014).

Then, it could be very tempting to conclude that the difficulty in addressing long-term challenges and decelerating the current course is somehow "hardwired" in *Homo sapiens'* evolutionary history, thus providing a convenient alibi for inaction.

## 6. Disarming an evolutionary trap: concluding remarks

In an environment that has been suddenly altered by human activities, an organism can make a maladaptive habitat (ecological trap), behavioural or a life-history choice (evolutionary trap) based on formerly reliable environmental cues, despite the availability of higher quality options. A trap arises when the organism is constrained by its evolutionary past to make a mistake, although suitable conditions (or adaptive choices) remain available elsewhere. In the short term, organisms are 'trapped' in their evolved proximate mechanisms and ecological interactions to respond to cues that now occur in a novel context (Schlaepfer et al. 2002, Robertson et al. 2013).

If we interpret the cognitive biases leading to our misperception of climate change as evolved proximate mechanisms (shaped in evolutionary time by our sociocultural NC), we can easily see that current climate breakdown fits into an evolutionary-trap perspective as defined above, with the sole specification that, besides other organisms (as seen in section 3), *we* are also making maladaptive behavioural choices in an anthropogenically altered environment. We've already tackled some of the consequences that are feeding back negatively on us and our life-supporting conditions.

Although a debate has been initiated on whether we are irreversibly trapped and we only need to admit that we can't prevent it any more (Franzen 2019), as we've previously seen in this paper, what characterizes *Homo sapiens*' sociocultural NC are its exceptional and wide-reaching learning abilities: its cultural evolution has long outclassed its biological evolution, and its creative and cumulative innovations have guaranteed the occupation of a niche that extends to the entire globe. Far from being doomed to a future of relentless maladaptive mistakes, *Homo sapiens* can embrace its transformative power and co-direct, through coordinate action, its own development and evolution, thus defining a safe-operating space on a finite planet.

This can be achieved by adapting the rules of the game that defines our behaviour and social interactions – *i.e.* our institutional forms (Powers et al 2019; Ostrom 1990) – as a modality of counteractive cultural niche construction aimed at deviating from the current maladaptive course of our previous, inceptive activities and at maintaining large-scale cooperation. As a species, we spent most of our existence leaving in small-scale societies characterized by intergroup competition and intense warfare, whereas our experience in progressively larger groups begins only 10.000 years ago, with the onset of agriculture: looking at our evolutionary history, the key driver of the transition to large-scale societies were self-created and selfenforced institutional rules, that ensured cooperation and coordination in large groups of unrelated individuals (Powers et al. 2016).

Besides traditional problems that characterize cooperation on a global scale and the management of common-pool resources (Ostrom 1990), such as the avoidance of inaction and free-riding, one of the major challenges for policy and institutional interventions in dealing with climate change consists in building the preconditions to cooperate with the future (Hauser et al. 2019). Because of the ecological inheritance of climate change, the public goods game posed by it is intergenerational: we need to provide for future generations to ensure the survival of nations, organizations, global ecosystems, genes (in this sense, there might be scope for applying the concept of evolutionary trap also in its narrow meaning). The assumption that individual actors act in a purely selfish way has been recently questioned (Hauser et al. 2019) and it seems that individuals are willing to invest in high-risk high-reward technology if necessary to mitigate and adapt to climate change (Andrews et al. 2018) – what is needed are institutional forms helping them doing so.

A further form of counteractive response to our detrimental, inceptive NC activities lays in the necessity of speeding up our innovative capacity to move away from carbon dioxide-producing emission systems and to ensure the removal of carbon dioxide already present in the atmosphere. There’s now a broad consensus that innovation is key to addressing the global challenge of climate change, both as regards its development and the diffusion on a massive scale of already available clean technology solutions (Rodyma-Taylor et al. 2013, IPCC 2018). The IPCC (2018, SPM, D.5.5) states with high confidence that the system transitions that are required to adapt to and limit global warming to 1.5°C include the widespread adoption of new and possibly disruptive technologies and practices and climate-driven innovation. Enhanced and pervasive technological innovation capabilities (also in industry and at financial level) are implied by the pursued system transitions. The development, commercialization and widespread adoption of mitigation and adaptation technologies can be supported both by international cooperation and national innovation policies, which can be more effective when combining public support for research and development with policy mixes that provide incentives for technology diffusion. Clearly, directed innovation and research cannot be pursued in the absence of adequate institutional change and effective management, so that these two points are strictly interrelated.

Innovation, defined in evolutionary terms as any learning process able to introduce new traits and to socially transmit new behavioural variants through the population (Cavalli-Sforza and Feldman 1981), has always been a defining feature of our species and, as previously mentioned in this paper (section 1), periods of climatic instability have coincided with evolutionary innovation and the adoption of new technologies also in our evolutionary past. What is required now is a massive effort in promoting what in cultural evolutionary literature passes under the term of 'guided variation', *i.e.* the non-random generation of cultural variation through learning, research or analogous endeavours (Boyd and Richerson 1985) (again, there's plenty of scope in approaching sustainability challenges through a cultural evolutionary perspective). If not properly managed and guided, evolutionary processes can take us where it would be advisable not to go. The climate challenge is ultimately a challenge about strengthening institutional capacity and drastically accelerating the pace of innovation at the global scale. The available knowledge on the consequences and the deep evolutionary causes of human impact on planetary systems, interpreted through the lenses of NC perspective, have the potential of providing a missing guide to institutional and societal strategies – a science of intentional change (Wilson et al 2014) that can take us out from current self-trapping course – also implementing effective communication to counter the unaware reliance on delusional misperceptions and to illustrate the pervasive evolutionary implications of climate breakdown.

## Acknowledgements

We thank Dr. Francesco Suman (University of Padua) for helpful discussion in the early phases of this work and Dr. Adrian Currie (University of Exeter) for his thoughtful feedback on a later draft of this manuscript. We would also like to thank the editor and the anonymous reviewers for their careful reading of our manuscript and their many insightful comments and suggestions.

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# 6.

# Conclusions

In this thesis I have discussed epistemic and evolutionary implications related to four main processes at the centre of current debate on modern human origins: the speciation of *Homo sapiens*, the transition to behavioural modernity, Neanderthal-*H. sapiens* admixture, human niche construction and long-term anthropogenic transformations applied to the context of the current climate crisis.

I have defended an *extended* single-origin for *Homo sapiens* on evidential and evolutionary grounds, arguing that the paleoclimatic and paleoenvironmental context of Middle Pleistocene Africa likely favoured an allopatric speciation process from a widespread and diversified ancestral population (Chapter 2). I have then moved to behavioural and archaeological side of the origin problem and analysed the evolution of the research agenda on "behavioural modernity", developing a philosophical account of "investigative disintegration" and criticizing approaches that have not kept up with new standards of explanatory adequacy (Chapter 3). Turning to palaeogenomic research, I have discussed evidence of archaic admixture with respect to the taxonomic status of *Homo sapiens* and Neanderthals and argued that distinct specific status is granted on the basis of a diachronic perspective on lineage divergence and multiple operational criteria (Chapter 4). Finally, I have framed anthropogenically-driven climate change as a niche construction process played at a global scale, having deep evolutionary roots and long-term consequences that today require us to produce a counteractive response to our prior actions to deviate from current maladaptive trend (Chapter 5).

In what follows, I would like to draw attention upon a few aspects that emerge *a posteriori*, also anticipating potential worries that the reader might have at this point and deriving some lessons that transversally intersect all the chapters.

## 6.1 Patterns of biological and cultural change

I have emphasized on several occasions that the evolution of morphological (Chapter 2) and of cultural traits (Chapter 3) are consistent with a mosaic pattern of change. In the context of our biological origins (the speciation process), I have argued that a mosaic diversification of traits among Middle Pleistocene ancestral groups is compatible with a local emergence of a more derived hominin form. However, in the context of the transition to a modern behaviour, not only I have argued that some proxies are cross-specific, but that the problem agenda has changed to such a point that Rubicon-based practices or the quest for first appearances have become inadequate, and the relevant explanatory weight is now carried by processes explaining the stabilization of human sociocultural niche. Although this may strike the reader as being somewhat contradictory, I believe there are good reasons for expecting a much less orderly and geographically circumscribed story for human behavioural and cultural evolution.

Despite being sympathetic towards attempts at finding unitary and integrative narrative of our origins (see for instance Kissel and Fuentes 2021), I still believe there are fundamental differences between biological and cultural channels of inheritance that demand different research questions. First, cultural transmission is known to be capricious, both as regards it not being limited to a vertical mode of inheritance (as human biological evolution *mostly* is) and the pace of change, which is not bound to biological generations and can be relatively rapid (although this is not a general rule: culture can be very conservative too). This translates into differences also as regards how stability is reached (Kronfeldner 2021): cultural repertoires, as we’ve seen (Chapter 3) can fluctuate considerably before approaching an equilibrium and innovations can be gained, lost and re-gained before becoming fully consolidated.

Second, cultural change can certainly be affected by biological change and can affect it by exerting selective pressures on hominins (via gene-culture coevolution). But cultural change and stabilization can happen independently from it. One central lesson we learned from the debate on behavioural modernity is that there’s no reason to posit a concomitant and causally related biological or genetic change to justify the appearance in the archaeological record of an innovation or a complex cultural repertoire. This is largely demonstrated by a general lack of direct correspondence in hominin phylogeny between biological and cultural novelties, speciation patterns and new technologies (and doubts can be also cast on MSA items being the sole expression of *Homo* sapiens, as seen in Chapter 2). The dynamism of material culture and its ability to travel across populations and taxa that heavily rely on their learning environment make it an untrustworthy proxy for taxonomic boundaries and biological classification purposes (as suggested in Chapter 4).

As regards the problem of our origins, it should be clear now why asking about biological speciation is different from asking about the fixation of cultural traits. In Chapter 2 I have underlined the importance of a geographic approach to biological evolution as spatial distributions and their context inform selective pressures, levels of gene flow, discontinuities and, ultimately, macroevolutionary patterns. The case of behavioural modernity, given the nature of cultural transmission and evolution, is less of a question about origins and first appearance of novelties – I have in fact criticized the practice of attributing special significance to new, earlier finds for expanding implicit Rubicons – and more of a question about how an emergent property becomes archeologically consistent and a threshold effect is reached.

This discussion should also clarify some terminological choices that have been made in writing this thesis. I have retained the expression “anatomical modernity”, while being conscious of the risks inherent in what may sound as a "prescriptive" approach to human anatomical variation and of the difficulties in distinguishing traits of modern humans from those of our ancestors. Identifying step changes (novel taxa) in the cumulative process of descent with modification (baseline evolution) is the hard problem of studying evolutionary change (cfr. Foley et al. 2016). However, the emphasis on the mosaic pattern of anatomical change among late populations of the LCA in Africa and on an extended single-origin serves to acknowledge the complexity of this process, but does not rule out the possibility of recognizing, at a different level, the core mechanism at the basis of hominin diversity, *i.e.* speciation. Moreover, the adjective "archaic" may appear to be somewhat confusingly used in literature to refer both to ancestral and contemporary species of *Homo sapiens*, in virtue of them displaying a set of plesiomorphic characters. Here it is retained for matters of convenience, without any immediate implication for the possibility of an archaic species of sustaining cultural complexity or otherwise.

## 6.2 Patterns of progress in paleoanthropological science

I want to discuss now another aspect that I think is revelatory of how paleoanthropology progresses as an historical science, drawing from the various evidential and epistemic contexts seen throughout this thesis. One crucial question in this sense is the relationship between the evidence base and the explanations: to what extent are narratives of human origins sensitive to new evidence?

Popular portrayals of human evolutionary research often speak of narratives being rewritten over and over again, revealing the profoundly rooted common sense that paleoanthropological knowledge is intimately provisional and that new findings have a high chance of revolutionising previously reached consensus and hypotheses. While this is not always entirely incorrect, the spectrum of possibilities is much more complex. This thesis has offered multiple examples in which the relationship between incoming data and explanations is instantiated in different ways. First, no matter how sophisticated the technology may be or how well-preserved some fossils remains are, there are rarely silver bullets in paleoanthropological reasoning that are exempted from reinforcement or calibration from other theoretical and empirical resources. Although much of the pan-African model hinges on the interpretation of the Jebel Irhoud material, it alone cannot have much disruptive power towards the single-origin hypothesis. It is in fact the tangle of heterogeneous lines of evidence that the Jebel Irhoud discoveries have promoted (and their use in corroborating the interpretation of other fossil sites like Florisbad) that is the object of my critical analysis in Chapter 2. Taken alone or in combination with other data, however, when evolutionary knowledge is mobilized, these discoveries still prove compatible with a more localized appearance of our derived anatomical form. But the overall narrative (which I termed *extended* single-origin) is enriched, and we have now a more detailed understanding of the different phases involved in the evolution of modern humans.

If under some circumstances evidence can be integrated, updating and complexifying interpretive scenarios, under others new pieces of information will fail to fit pre-existing schemas. Patterns of progress in paleoanthropology are tricky and debates may not follow a smooth trajectory, radically reshaping initial research questions and practices along the way.

I have argued that this is something that happened for behavioural modernity (Chapter 3) and I have briefly mentioned how the jigsaw puzzle metaphor fails to capture these peculiar dynamics of research. Although Chapman and Wylie (2016, pp. 3,11) refer to it as a hackneyed analogy often used to depict the practice of archaeological interpretation, I believe this criticism can be extended to misrepresentations of the complexity of research dynamics in paleoanthropology.

In the case of behavioural modernity, decades of anomalous data not only have failed to fit in the Upper Paleolithic revolution scenario as missing pieces of a perfectly functioning narrative but have restructured the already assembled picture. Not only the relevant problem to be solved has changed, but the context-dependency of cultural trajectories require now to interrogate the interplay among biology, cognition, demography and sociocultural factors at a regional scale. So, there's hardly just one puzzle to be solved, although trends can be revealed when viewed at a broader level of analysis (cfr. D'Errico and Banks 2013). Clearly, as it often happens during phases of destabilization, practices change at different speeds and although new criteria of explanatory adequacy have been established, Rubicon-based approaches have not been completely abandoned.

A third example of interaction between an expanded evidence base and an explanation is provided by Chapter 4. If it's indeed possible to recognize recurring questions and debates in paleoanthropology – the core topic of this thesis is perhaps the most blatant example – this does not mean that no progress has been made. Iterating the same question in a changed epistemic context mean testing, strengthening, or calibrating previous answers, as in the case of the hoary issue of whether *Homo sapiens* and Neanderthals constitute separate species. This is true as long as all the available epistemic resources are used (like evolutionary biology inputs on incomplete reproductive isolation among sister taxa). This iteration and persistence of questions across time and changing research agendas is no symptom of knowledge stagnation, but a healthy practice of shaking up inferences and developing new ways of seeing data.

## 6.3 Future directions

Interrogating modern human origins doesn't mean tackling questions pertaining to one single evolutionary history. Developments of the past years have opened up new, exciting vistas on the role of other hominin forms in the evolutionary history of *Homo sapiens*, and most obviously of the Neanderthals. In this thesis I have only discussed quite straightforward implications of evidence of Neanderthal ancestry in contemporary non-African individuals. But there are other avenues of investigation that have expanded their evidential basis, with new explanations currently gaining traction in the scientific debate.

For instance, hypotheses surrounding the fate of the Neanderthals have changed considerably over time and in particular as regards the share of blame that *Homo sapiens* should take. Paleogenomic data in the last decade provided informative clues also about Neanderthal population sizes and history, and a heightened risk of extinction has been suggested based on population dynamics, disconnectedness among demes and genetic diversity alone (in particular, estimates of effective population size; cfr. Prüfer et al. 2014, 2017, Mafessoni et al. 2020). This has promoted "demographic explanations" for the demise of the Neanderthals, frequently presented as null hypotheses against which competing, and "less parsimonious" hypotheses – replacement by competitive exclusion or extinction by climatic and environmental factor – are to be assessed (Vaesen et al. 2019, 2021). However, the degree to which demographic features can be disentangled from competitive exclusion or environmental effects and the explanatory relationship between demography and extinction requires further analysis (manuscript n. 9 listed in the Appendix provides a first attempt in this sense).

Related to this is the debate on the cognitive and cultural prowess of our evolutionary cousins. I have only tangentially discussed some problematic assumptions in Chapter 3 in relation to behavioural modernity. Much literature has framed the issue in comparative terms, from much criticised hypotheses supporting a cognitive, intrinsic "superiority" of modern humans to others claiming a cognitive indistinguishability in archaeological terms (Villa and Roebroeks 2014, Wynn et al. 2016). Rejecting the first position, however, does not commit to automatically accept the second, as there is indeed no reason why should conceive only one way of instantiating "being human". Prior to any possibility of comparison, fundamental questions need to be asked about how to squeeze cognitive abilities, differing capacities or an entire spectrum of cognitive possibilities out of material traces, especially if these are not strongly biologically and genetically canalized.

Crucial epistemic questions lay at the basis of the very possibility of investigating the many ways of being human that have been explored throughout hominin evolutionary history.

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# Appendix

## Complete list of publications and submitted manuscripts during the Ph.D. programme

1) **Meneganzin A**., Pievani T., Caserini S. (2020) Anthropogenic climate change as a monumental niche construction process: background and philosophical aspects. *Biol Philos* 35**,** 38. https://doi.org/10.1007/s10539-020-09754-2

2) Pievani T., **Meneganzin A**. (2020). *Homo sapiens*: The First Self-Endangered Species. In: *People, Nature and Environments: Learning to Live Together*; eds: Ana Cristina Roque, Cristina Brito & Cecilia Veracini. Newcastle upon Tyne: Cambridge Scholars Publishing. ISBN-13: 978-1-5275-4131-3

3) Kuschmierz P., **Meneganzin A**., Pinxten R. Pievani T, Cvetković D., Mavrikaki E., Graf D., Beniermann B. (2020). *Evolution: Education and Outreach*. Towards common ground in measuring acceptance of evolution and knowledge about evolution across Europe: a systematic review of the state of research. https://doi.org/10.1186/s12052-020-00132-w

4) Currie A., **Meneganzin A**. (*in press*). Hawkes' Ladder, Underdetermination & the Mind's Capacities. Book chapter. In *Oxford Handbook of Cognitive Archaeology*. Eds: Thomas Wynn, Karenleigh Overmann, and Frederick Coolidge. Oxford University Press.

5) **Meneganzin A**., Pievani T., Manzi G. Pan-Africanism vs single-origin of *Homo sapiens*: brining the debate back to evolutionary biology. *Under review (Evolutionary Anthropology).*

6) **Meneganzin A**., Currie A. Behavioural modernity, investigative disintegration and Rubicon bias. (*in press*). *Synthese.*

7) Kuschmierz P. … **Meneganzin A.** … et al. (2021). European first-year university students accept evolution but lack substantial knowledge about it: a standardized European cross-country assessment. *Evolution: Education and Outreach 14:17.* https://doi.org/10.1186/s12052-021-00158-8

8) **Meneganzin A.**, Bernardi M. Were Neanderthals and *Homo sapiens* 'good species'? *Under review (Systematic Biology)*

9) Currie A., **Meneganzin A**. Not by demography alone. Neanderthal extinction and null hypothesis in paleoanthropological explanation. *To be submitted.*