Reconstructing Soft Tissues of Plio-Pleistocene Hominids using Comparative Anatomy of Modern Humans & Great Apes

A thesis submitted by

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Abstract

The aim of facial approximation is to recreate the appearance of an individual from their dry skull. This technique has often been used following the discovery of a new species of ancient hominid, such as those belonging to the Australopithecus or Paranthropus genera. Facial approximations provide a 3D model for these species and provides another means for scientists to understand the morphological differences between and variations among archaic hominids and modern humans. These models, which are often produced three-dimensionally, also help to guide public attention towards biological anthropology and to disseminate scientific facts about human evolution. Unfortunately, sufficient attention has not been paid to the inconsistencies in the depictions presented nor how facial approximation techniques may be affecting the legitimacy of the knowledge disseminated through their use.

The primary aim of this thesis was to develop more reliable methods for approximating the facial soft tissues of Plio-Pleistocene hominids. This was accomplished by identifying bone and soft tissue covariation patterns in the head of primates, including modern humans, and applying these relationships to Plio-Pleistocene hominid skulls. The overarching hypothesis for this thesis was that if homogeneity of covariation between soft tissues and its underlying bone can be observed among primate species, including modern humans, then these relationships can be extrapolated to Plio-Pleistocene hominids. Such relationships will improve the biological accuracy of their depictions and reduce the problem of inconsistency currently burdening the practice of ancient hominid facial approximation.

In Chapter II, it will be shown how archaic hominid facial approximation, as it had been established before the restorative findings of this thesis, had become a domain of artists, who included various theoretical interpretations of human evolution into the facial approximations they produced without questioning their scientific legitimacy. Chapters III and IV showcase how artistic intuitionism no longer suffices to illustrate the facial appearance of our ancestors. In these chapters, new statistical methods that more reliably approximate the facial soft tissue thicknesses for Chimpanzees (*Pan troglodytes*), Bonobos (*Pan paniscus*), and by extension other Pliocene hominids, such as

Australopithecus africanus, are presented. In addition, new methods for predicting nasal protrusions for all African great apes, modern humans, and by extension all ancestors leading to these clades are also presented. Finally, in chapter 5, general thoughts on some lingering complications and the future of the practice of hominid facial approximation are discussed.

The original contributions to knowledge contained within this thesis could not have occurred without challenging the status quo. By hypothesising that the facial soft tissues Plio-Pleistocene hominids could be scientifically reconstructed this thesis has made new discoveries that has in-turn encouraged the field to advance into an empirical discipline from one that was predominately an intuitive artistic activity. Thus, this thesis marks the beginning of a new era of evolutionary reconstructions in the field of biological anthropology.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Ryan M. Campbell

Signature: ___ ______________________________ **Date:** 17 / 05 / 2022

Dedication

This thesis is dedicated to the great apes. These species are critically endangered. The minimum count of mountain gorillas (*Gorilla beringei beringei*) inhabiting the Bwindi Impenetrable National Park in Uganda, as well as the Sarambwe Nature Reserve in the Democratic Republic of Congo is extremely low. The total number of wild mountain gorillas, including the mountain gorillas inhabiting the Virunga Mountain range of Rwanda and Congo, is estimated to consist of only 1063 individuals. At the time of writing this thesis, there were no mountain gorillas in captivity. All attempts to house these animals have resulted in premature mortality. We do not yet know why mountain gorillas cannot be housed in captivity but until a reason and solution is found, captive breeding programs for mountain gorillas are not an option. Currently, therefore, conservation projects can only occur in the mountain gorillas' native environments, which continues to be disturbed because of human population growth. Similarly, the total number of wild Tapanuli Orangutan (*Pongo tapanuliensis*), which is the third species of Orangutan alongside *Pongo pygmaeus* and *Pongo abelii*, is estimated to consist of a mere 800 individuals. By comparison, the current world population of modern humans is currently upwards of 7.9 billion.

It is simply not possible to overemphasise the importance of savings the lives of these animals. Writing this thesis has made me feel more compassion towards our great ape cousins than ever before. I hope that my research will inspire future generations to lead conservation initiatives for it is highly probable that without these the great apes will not survive.

Acknowledgments

This thesis could not have occurred without the support and encouragement of countless people. I have done my very best to acknowledge all who made this work possible. I would like to acknowledge my supervisors Maciej Henneberg, Jaliya Kumaratilake, and Fernando Marmolejo-Ramos—it has been an absolute pleasure working with all of you; my colleague and best friend Gabriel Vinas—may we continue to grow as scientists and carry on approximating hominids for years to come; Ellie Simpson for facilitating the acquisition of human data; Zoos South Australia, Kyoto University and Duke University for permitting access to primate material; Stefano Benazzi and the website administrators for *African Fossils* and *HETMP* for sharing digital scans of hominid fossils; Ian Linke and Hayden Westell for allowing me to use the 3D printing lab, as well as Victor Surovec and Dan Collins; Michael Dutkiewicz and John Engelhardt for producing the illustrations of hominid skulls included in this thesis; Hugh Kearns for helping me to stay on track during the course my PhD; my beautiful wife, Iulia, who has supported my scientific pursuits every single day; and the editors and reviewers of *Frontiers in Ecology and Evolution* and *PLoS ONE* for processing and providing comments on the manuscripts included in this thesis. Lastly, and most importantly, I would like to acknowledge the chimpanzee, bonobo, gorilla, orangutan, siamang, and baboon who are included in this study. Without you, this thesis would not be possible.

Research Contributions

Publications Directly Resulting from this PhD

Campbell, R.M., Vinas. G., Henneberg, M., and Diogo, R. (2021). Visual depictions of our evolutionary past: A broad case study concerning the need for quantitative methods of soft tissue reconstruction and art-science collaborations. ***Frontiers in Ecology and Evolution***, 9(60).

Campbell, R.M., Vinas. G., and Henneberg, M. (2021). Towards the restoration of ancient hominid craniofacial anatomy: Chimpanzee morphology reveals covariation between craniometrics and facial soft tissue thickness. ***PLoS ONE***, 16(6).

Campbell, R.M., Vinas. G., and Henneberg, M. (2021). Relationships between the hard and soft dimensions of the nose in *Pan troglodytes* and *Homo sapiens* reveal the nasal protrustions of Plio-Pleistocene hominids. ***PLoS ONE***, 17(2).

Conference Presentation Related to this Thesis

Campbell, R.M., Vinas. G., and Henneberg, M. (2021). Comparative analysis of pronasale position in *Pan troglodytes* and *Homo sapiens* reveals the nasal protrusions of Plio-Pleistocene hominids. Institute of Evolutionary Medicine (IEM), University of Zurich, 5th December, Zurich, Switzerland.

Note* this presentation was delivered as part of a public online event via Zoom for the IEM from The University of Adelaide, Australia.

Other Speaker Invitations

Campbell, R.M., Vinas. G., and Chagi, S. (2021) The Story of Us. Episode 26: Hominin Reconstruction. Retrieved December 6, 2021, from World of Palaeoanthropology https://worldofpaleoanthropology.org/storyofus/

Chapter 1: Introduction

1.1 Biological anthropology and comparative anatomy

Biological anthropology is the study of humans as biological organisms and comparative anatomy is the main foundation upon which our knowledge of human evolution is based. Human evolution is the story of change that occurred in a single lineage over a relatively short period of time. No other species has received the same amount of attention as our own. There are estimated to be 1.5 million beetle species (Stork et al., 2015), yet not one of them has inspired the same academic interest as *Homo sapiens*: the species to which we belong. All animals, including beetles and humans, are connected by a common family tree, which is divided into clades formed by multiple branches reflecting various degrees of similarity among species. While beetles might not have received the same degree of interest as *Homo sapiens*, other species have, particularly those species who are closer to us morphologically due to a recent common ancestry.

The great apes, which includes bonobos, chimpanzees, gorillas, and orangutans, are the closest extant relatives to modern humans and hold a more common evolutionary heritage with us than any other species of primate. For this reason, great apes have been the focus of countless studies attempting to answer central questions related to the evolution of the modern human lineage (hominins). Modern humans, great apes, and all ancestors leading to these clades are collectively referred to as hominids and are members of the superfamily Hominoidea. The hominin lineage, which is our own lineage, separated from chimpanzees and bonobos (panins) approximately 7-8 million years ago (Diogo et al., 2017; Langergraber et al., 2012), from gorillas (gorillinins) approximately 10 million years ago (Scally et al., 2012), and from orangutans (ponginins) perhaps 12-16 million years ago (Chen and Li, 2001). Hence, *Homo sapiens* are not descendants of great apes but share a common ancestor with each of these clades. Ancestors in the human lineage are called hominins and most of our knowledge of hominins comes from fossils from the Pliocene and Pleistocene, two epochs that are commonly combined and referred to as the Plio-Pleistocene. It is generally accepted that by understanding more about great apes today, more can be known about human ancestors from the past (Goodall, 1999)

Comparative anatomy of humans and great apes is an essential tool for making evolutionary inferences about Plio-Pleistocene hominids. An evolutionary inference is the acceptance of a hypothesis reached on the basis of existing evidence and principles of scientific inquiry. All knowledge about human evolution is built upon inferences. For example, based on evolutionary theory and the hundreds of skeletal remains that now make up the hominin fossil record, it can be inferred that modern *Homo sapiens* came into existence through the process of evolution. While this inference may lie closer to absolute certainty, others are not so easily measured. Archaic hominid locomotion, growth trajectories, hunting and scavenging behaviour, grooming habits, adaptive radiation, and genetic diversity are but a few examples of knowledge that is much harder to infer because we cannot directly observe this knowledge in the fossil record.

It is important to state at the outset of this thesis that however well-preserved and intricate the fossil record is, or generally agreed upon their phylogenetic positions may be, it is misleading to call inferences about human evolution facts. Any thoughtful scientist will recognize that constructed facts are injurious to science because they cannot, by definition, be changed. Biological anthropology, and science in general, thrives in the empirical correction of previously accepted ideas, although this usually takes time as new discoveries are made and/or new technologies are developed (Popper, 1934, 1972). This by no means relegates evolutionary knowledge to a purely negative category, it just means that scientists need to exercise an extra level of caution when using present day observations to infer the past. This thesis has been constructed with these overarching guidelines in mind.

We can best sense the incremental adjustment of ideas in practice using examples of when previously accepted assertions were modified. The story of Piltdown man is an outstanding example because it practically embodies this phenomenon. Piltdown man is the nickname given to two bones that were discovered in 1912 in England by Charles Dawson (Dawson and Woodward, 1913). The bones consist of a human-like cranium and great ape-like mandible. The presence of these features led Sir Arthur Keith, an honoured British anatomist and physical anthropologist at that time, to announce the find as a newly discovered species named *Eoathropus dawsoni*. Along with the belief that the fragments belonged to a missing link between man and ape, Keith believed that the modern human lineage originated in The United Kingdom of Great Britain. This idea would persist for the next 43 years until the true nature of the Piltdown fossil was revealed. New dating methods based on fluorine levels revealed that the fossil was much younger than initially reported. Furthermore, microscopic examination of the molars revealed marks left from files that had been used to flatten the molars deliberately, and the aged appearance of the skull was revealed to be nothing more than potassium bichromate pigment. In the end, Piltdown man was declared a forgery. The cranium was found to belong to a modern human and the mandible to an orangutan (Millar, 1972). This correction in scientific thought is now regarded as a triumph of scientific enquiry. It is important to state that there was not a single point in time when the forgery was announced, rather this revealed itself gradually over a discussion that lasted decades.

To continue this line of thought, consider that there was once a time when chimpanzees were referred to as protohumans. The discovery of *Ardipithecus ramidus* and subsequent comparison with chimpanzees showed that this is not the case because many chimpanzee traits are derived, i.e., not inherited from a common ancestor (Lovejoy, 2009; Suwa et al., 2009). Comparative anatomy facilitated this correction in scientific thought and this thesis is built upon the foundation of this discipline.

1.2. Visual images as a means of disseminating scientific knowledge

Comparative anatomy is primarily a descriptive field although images have been readily used to compliment descriptions for centuries. One particular example relevant to this thesis dates back to the 17th century. In 1699, before the advent of photography, engravings were used to print illustrations. British naturalist Edward Tyson, who is regarded as the founder of modern comparative anatomy, commissioned Dutch artist Michael van der Gucht to produce a series of engravings for a philosophical essay titled *The Anatomy of a Pygmy compared with that of a Monkey, an Ape, and a Man* (**Fig. 1.1.**). The illustrations were intended help disseminate the anatomical knowledge that Tyson had acquired during his dissections of what was then referred to as a *Pigmie* but is now known as a chimpanzee. The engravings were produced using a live chimpanzee as reference, although there appears to be a devoted effort to depict the animal as subhuman. There is asymmetry in the face accompanied by amblyopia, a foolish smile, and the inclusion of a cane to support the animal in upright posture. One cannot know for sure the philosophical or psychological preference for representing the animal in this way, although Tyson likely tailored the illustrations to depict the animal in accordance with the ideological assumptions of the time (Edward, 1699).

Fig 1.1. Michael van der Gucht's engraving of a chimpanzee commissioned by British naturalist Edward Tyson for the philosophical essay titled *The Anatomy of a Pygmy compared with that of a Monkey, an Ape, and a Man* (1699).

The mischaracterization of non-human apes as primitive humans was an idea that arose shorty after Charles Darwin (1859) published his seminal work *On the Origin of Species by Means of Natural Selection*. This was probably not a view shared by everyone, but it was certainly shared by those who had an interest in separating us from other animals. Nothing illustrates the mischaracterization of great apes more clearly than the depictions that were produced by the French sculptor Emmanuel Frémiet (Pierce, 2018; Pollack, 2020). The bronze and marble representations of the gorilla (**Fig 2.1.**) and orangutan (**Fig 3.1**) preserve how these animals were perceived during the time in which they were created. By comparing these representations though time, the influence that scientific research had on the perception of our great ape cousins is made clear. Studies on Koko, a female lowland gorilla (*Gorilla gorilla*), who learned to communicate thousands of words between herself and her teachers using sign language, no doubt contributed to the change in the characterization of the gorilla, from one that had depicted her species as savage and unintelligent to one that more fairly recognized the gorillas' high intellectual, emotional, and social development (Patterson et al., 1988).

Fig 2.1. Emmanuel Frémiet, *Gorilla carrying a woman*, 1887.

Fig 3.1. Emmanuel Frémiet, *Orangutan strangling a Borneo savage*, 1896. This marble sculpture was completed to decorate the exterior of the new galleries of comparative anatomy, palaeontology, and anthropology at the Natural History Museum in Paris.

Neandertals, also referred to as Neanderthals, are another example of ideological assumptions affecting representation of a species. Neandertals (*Homo neanderthalensis*), who existed between 350,000 and 40,000 years ago, were once depicted as inferior to modern humans. The type specimen for this species (Feldhofer 1; found in 1856 in Germany) exhibits a large brow ridge and post-orbital constriction. Because these features are present in great apes, scientists erroneously connected their presence in Neanderthals with species-wide idiocity. Illustrations of Neanderthals built around this ideology depicted them as unhygienic, poorly groomed brutes (Anderson, 2011). Scientists now recognize, thanks to genetic data and a plethora of archaeological material including intricate cave paintings, fishing tools, and skeletal remains, that Neandertals did not go extinct because of their inferior intellect or were replaced my modern humans. Instead, it was interbreeding and assimilation that was responsible for the disappearance of the Neandertal morphology from the fossil record (Saniotis and Henneberg, 2010). Illustrations of Neandertals today present people like us, not dissimilar from modern day human tribes.

1.3 Anthropological facial approximation

Anthropological facial approximation, also referred to as facial reconstruction, and the topic of this thesis, dovetails nicely with both biological anthropology and comparative anatomy. This practice was developed as a last resort in forensic science to support the investigation and identification of an individual from a dry skull. The practice is also used in palaeoanthropology to produce portraits of ancient people from the past, including Plio-Pleistocene hominids. An understandable criticism of this practice is that a facial approximation undertaken on an archaic hominid skull cannot be tested for its accuracy. However, while it is true that metric assessment of soft tissue depths at various cephalometric landmarks cannot be directly compared to the hominids in question, scientists are yet to explore how metric assessments may be verified indirectly from assessments of extant apes. If commonalities could be identified in living apes, then these commonalities may be interpolated into archaic hominids with a reasonable degree of confidence. This is the aim of this thesis and follows the guidelines discussed previously regarding how inferences are made about human evolution using observations of present-day phenomena.

1.4 Aims and objectives of this thesis

Accurate presentation of the evolutionary process that produced modern humans is of utmost importance. Evolutionary theory provides a story of our place within the natural world, which affects the way people perceive themselves and their lives. It is therefore important for the story to be disseminated in its truest form and to avoid perpetuating false facts that are highly injurious to public trust in science. Since facial approximations of hominids are used in science dissemination, there is a need to hold the practice to the same level of scrutiny as peer-reviewed research. Science thrives upon the continuous correction of error. Most errors arise from inadequate knowledge of the empirical world because we have no methods of obtaining this knowledge. Artists need to understand that from a scientific standpoint their facial approximations are not immune to error. Thus, this thesis sets out to firmly establish archaic hominid facial approximation as a scientific activity by testing, evaluating, and improving upon current methods, as well as producing new techniques, based on primate comparative anatomy.

This thesis includes 3 manuscripts, all of which have been published in peer-reviewed academic journals. Reprints of the publications are presented in the relevant chapters of this thesis. The first manuscript (Chapter 2) is a review article covering the full breadth of the literature on anthropological facial approximation, from the first approximations produced by Mikhail Mikhaylovich Gerasimov to the present-day approximations produced by John Gurche, Élisabeth Daynès, and Adrie and Alfrons Kennis. In addition to providing a comprehensive overview, this manuscript includes preliminary research that was carried out by the author of this thesis over the last seven years. The second manuscript (Chapter 3) is an original research article that presents soft tissue depth data for chimpanzees and is the first study to show covariation between hard and soft tissues in non-human hominids. This chapter also includes a set of regression equations that can be used to approximate the faces of chimpanzees, bonobos, and extinct hominids with similar craniometrics as these species. The third and final manuscript (Chapter 4) is another original research article that presents a method for approximating the nasal protrusions for hominids. This method can be used to approximate the nasal protrusions for modern humans, all African great apes, and by extension all Plio-Pleistocene hominids. The final chapter of this thesis (Chapter 5) provides a reflective summary of the previous chapters. It also provides a discussion of the lingering complications and goals for the future of hominid facial approximation, as well as framework for constructing future soft tissue approximation methods with interspecies compatibility.

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Chapter 2: The Review

Visual depictions of our evolutionary past:

A broad case study concerning the need for quantitative methods of soft tissue reconstruction and art-science collaborations

Ryan M. Campbell, Gabriel Vinas, Maciej Henneberg, and Rui Diogo

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Context of Review Article

Reconstructions of Plio-Pleistocene hominids have become increasingly popular in recent years, particularly those key species on the branch of the tree of life to which we belong. The use of such reconstructions has been considered as an effective translator of scientific knowledge, as they represent a synthesis of information that is more accessible and comprehensible to the general public. Therefore, their role in disseminating discoveries and advances in the field of biological/physical anthropology is of fundamental importance.

The aims of this research were to provide a comprehensive review of the approaches involved in the production of hominid reconstructions, from the early nineteenth century to modern-day forensic and computer-based methods, and to allow for future directions to be established. This research also provides a review of the broader societal implications of presenting visual depictions of hominids that are not based on strong scientific foundations.

The basis for this review stemmed chiefly from the work carried out by myself and one of my long-term colleagues (Gabriel Vinas) over last six years attempting to produce our own reconstructions. As these preliminary studies show, the practice is mostly based on methods that are irreplicable resulting in gross discrepancies between reconstructions of the same individual. So severe are these discrepancies that it is almost as though previous practitioners had never encountered a single hominin reconstruction before commending their own.

As the present manuscript was intended from the outset to be read within the context of an eBook, the text includes references to the “special issue” to which this manuscript was enclosed, but the content stands on its own and can be read as such.

This is the first time that such a formal survey and systematic analysis of the literature has been conducted on this topic. Therefore, the resulting manuscript provides value as a kind of *vade mecum* that will be useful to all those who are involved in the detailed, albeit exciting, work of reconstructing the appearances of our ancestors.

Statement of Authorship

Title of Paper: Visual depictions of our evolutionary past: A broad case study concerning the need for quantitative methods of soft tissue reconstruction and art-science collaborations

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Contribution to the Paper: Ryan M. Campbell initiated the investigation into scientifically accurate hominin reconstructions, analysed the literature, wrote the majority of the manuscript, and edited the whole version of the manuscript.

Overall percentage (%): 85%

Certification: This paper reports on original research I conducted during the period of my higher degree by research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.

Signature: _______ ________________________ **Date:** 10 / 09 / 2021

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. The candidate's stated contribution to the publication is accurate (as detailed above);
ii. Permission is granted for the candidate to include the publication in the thesis; and
iii. The sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author: Gabriel Vinas

Contribution to the paper: Gabriel Vinas wrote the section under the heading "The Ethics of Reconstruction and Societal Implications", carved the sculpture featured in Figure 8, modelled all reconstructions featured in Figures 1-7 in partnership with Ryan M. Campbell, and edited the whole version of the manuscript.

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Name of Co-Author: Maciej Henneberg

Contribution to the paper: Maciej Henneberg advised the reconstructions featured in Figures 2-7, was involved in the six-year partnership reconstructing hominins with Ryan M. Campbell and Gabriel Vinas and edited the whole version of the manuscript.

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Name of Co-Author: Rui Diogo

Contribution to the paper: Rui Diogo had the idea of doing this manuscript for the special issue titled "Tetrapod Water-Land Transition: Reconstructing Soft Tissue Anatomy and Function", wrote the section under the heading "Introduction: Why Study and Reconstruct Muscles?", and edited the whole version of the manuscript

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Visual Depictions of Our Evolutionary Past: A Broad Case Study Concerning the Need for Quantitative Methods of Soft Tissue Reconstruction and Art-Science Collaborations

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Flip through scientific textbooks illustrating ideas about human evolution or visit any number of museums of natural history and you will notice an abundance of reconstructions attempting to depict the appearance of ancient hominins. Spend some time comparing reconstructions of the same specimen and notice an obvious fact: hominin reconstructions vary in appearance considerably. In this review, we summarize existing methods of reconstruction to analyze this variability. It is argued that variability between hominin reconstructions is likely the result of unreliable reconstruction methods and misinterpretation of available evidence. We also discuss the risk of disseminating erroneous ideas about human evolution through the use of unscientific reconstructions in museums and publications. The role an artist plays is also analyzed and criticized given how the aforementioned reconstructions have become readily accepted to line the halls of even the most trusted institutions. In conclusion, improved reconstruction methods hold promise for the prediction of hominin soft tissues, as well as for disseminating current scientific understandings of human evolution in the future.

Keywords: artistic license, facial approximation, hominid, hominin, hard tissue, soft tissue

INTRODUCTION: WHY STUDY AND RECONSTRUCT MUSCLES?

At a time in which we are increasingly exposed to acclaims about new powerful genetic tools in the media and academia, one may wonder as to why we would focus on muscle reconstructions at all in this introductory paper of this special issue. This is particularly the case since genetic tools are now being used in studies that have been typically done with anatomical tools in the past, such as those concerning phylogenetic reconstructions. Actually, molecular tools are now being used to undertake facial reconstructions, an area that was exclusive to anatomy until very recently. In September 2019, newspapers across the globe reported with astonishment that a new method based on DNA information recovered from the remains of extinct individuals known as the Denisovans enabled scientists to give them a face. Namely, those scientists gleaned anatomical clues from ancient genomes to put together a rough composite portrait of a young female that lived at Denisova Cave in Siberia 75,000 years ago (Gokhman et al., 2019), despite the fact that only small fragments of bones and teeth of Denisovans were found and their skeletal anatomy has not been documented. We will obviously not discuss here the details of that paper and its artistic repercussions, nor the way in which it affected the way Denisovans are perceived by the broader public, although we will briefly refer below to some other similar studies. Rather, the point is that, if we have all these new tools, including eventual facial reconstructions in the future, are anatomical fossil reconstructions destined to become unimportant? The answer is that this is not at all the case; as will be seen in the present paper, and in this special issue as a whole, it is in fact the opposite. There has been a renewed interest in such reconstructions, using new methods and expanding them to tissues other than skeletal ones, such soft tissues like muscles, arteries, veins, and nerves, making them more complete and comprehensive than ever before. This special issue is, in itself, the proof of that, as it would have been difficult to do a whole issue with so many papers from top scholars completely dedicated to muscle reconstructions a few decades ago. In fact, this new interest in fossil muscle reconstructions is part of a resurgence of the study of comparative anatomy *per se*—the now re-awoken "sleeping beauty", to paraphrase Virginia Abdala—which was in great part a by-product of the rise of Evo-Devo in the past decades (Diogo, 2018).

Some years ago, one of us, with Bernard Wood (Diogo and Wood, 2013), published a paper summarizing why the study of muscles continues to be extremely important for not only Evo-Devo, but also for evolutionary biology, anatomical sciences, biological/physical anthropology, and many other fields. As noted in that paper, a major reason why molecular tools have not yet completely eclipsed anatomical ones in studies of evolutionary relationships is that it is still not possible to recover DNA for most of the millions of species that became extinct much before the time that Denovisans did. For instance, no DNA has been recovered for the fossil taxa that are the central focus of this special issue; those representing the transitions from fishes and early tetrapods. Therefore, phylogenetic works of such groups have been traditionally done mainly with bones but are also increasingly using soft tissues—particularly muscles as will be seen in this issue. One of the reasons for this is, as noted in that paper, studies by us and various other authors on the whole osteichthyan clade (bony "fish" plus tetrapods), and on specific groups such as our own (primates), have shown that although osteological structures often provide more potential characters for phylogenetic analyses, myological characters tend to be more useful for inferring the phylogenetic relationships among higher clades.

Indeed, this seems to apply even to fossil taxa such as non-avian dinosaurs (e.g., Dilkes, 2000). This therefore illustrates how crucial it is to undertake accurate muscle reconstructions of fossils, to not only understand their functional morphology, and biology as a whole—bones do *not* move without muscles—but to also learn more about their evolutionary relationships, history, and adaptations. This is moreover crucial, as will be discussed below, for science dissemination and the way the broader public perceives those fossil taxa, such as early tetrapods, dinosaurs, and even the closest extinct relatives of the human lineage. We are thus living in a fascinating time in which instead of a decrease of interest in muscles, there is an exponential interest in developing new tools and ways to reconstruct them more accurately in fossil taxa, and in displaying them artistically in the web, dissemination books, popular movies and documentaries, and museum fossil displays. Due to the particular interest in the reconstructions of fossils of our human lineage for all these types of media, their artistic repercussions, and the way they influence the public perception and narratives built around them—including, unfortunately, racist and misogynistic ones, as shown in Moser's (1996) book *Ancestral images: the iconography of human origins*—in this introductory paper we will focus on our own lineage. The idea is to show that the focus of this issue, muscle reconstructions, has not only scientific repercussions, but also societal and artistic implications. As will be shown in sections below, such reconstructions involve major complexities and difficulties, but also bring fascinating new opportunities.

Over the last century, there has been a huge interest in reconstructing the face of members of our human lineage that lived many thousands, or even some millions, of years ago. However, most of these are based on unfalsifiable ad hoc stories that have little or no empirical evidence. For instance, it has been said that the prognathic faces of *Australopithecus* were more similar to our closest living relatives, the great apes (chimpanzees, gorillas, and orangutans), than to anatomically modern humans. Based on this observed similarity, some have assumed that the soft tissues covering their faces would also have been more similar to those of apes than to those of *Homo sapiens* (Aiello and Dean, 1990; Gurche, 2013). This kind of rhetoric, which is largely untestable, is frequently deployed in the process of reconstructing Plio-Pleistocene hominins (N.B., in this paper hominins means all humans since we split from common ancestors with separately evolving lineages). It is based on a kind of interpretation called retrodiction, which is an intuitive method for predicting the past based on present observations of natural phenomena. It is based on Charles Lyell's uniformitarian principle underlying evolutionary science. But how reliable is retrodiction? Could not this rhetoric be questioned? Here, we review the practice of hominin reconstruction from a scientific perspective and address some of its broader implications. Specifically, we begin by presenting some of the earliest examples of hominin reconstruction followed by a review of the current methods used. We then show where future research holds promise for improving existing methods and producing scientifically accurate reconstructions, followed by a discussion of our own view on the ethical and societal implications of artistic interpretations of hominins. Our aim is to identify areas where fresh research is needed, which can be applied to other non-human or non-primate taxa.

Our fascination with hominin reconstructions—and the basis for this review—stems chiefly from the work carried out by two of us (RC and GV) over the last 6 years attempting to reproduce 3D reconstructions of extinct hominins often using the muscle data that have been recently made available for apes by another co-author (RD) and his colleagues. Although many 2D reconstructions of hominins exists, which are arguably just as important as 3D reconstructions, we will focus mainly on 3D reconstructions as these are the ones that we have spent the most time trying to replicate. It is hoped that including our own reconstructions in this review will help to expose the limitations of existing methods and to substantiate our claim that the practice is lacking a robust scientific and empirical foundation. As we shall show, many of the questions regarding the appearance of Plio-Pleistocene hominins are yet to be answered and most, if not all, reconstructions are based on methods that are irreplicable. This once again highlights the difficulties and complexities of muscle reconstructions but also the enormous opportunities that we now have to make progress in the area of muscle, facial, and whole-body reconstructions.

A BRIEF HISTORY OF HOMININ FACIAL RECONSTRUCTION

The earliest reconstructions of hominins were carried out in the late nineteenth and early twentieth centuries by artists and scientists in the form of both 2D and 3D portraits as well as whole-body reconstructions, produced soon after the discovery of various fossils. As very few hominin fossils have ever been found—it is, after all, a well-known fact that there are more active physical anthropologists today than there are hominin finds—it is relatively easy to compare reconstructions of the same individual. As we shall show, there are only a handful of well-preserved skulls suitable for reconstruction, which not only makes it easy to compare appearances between reconstructions of the same individuals produced by separate practitioners, but also highlights the role of how individually constructed knowledge about human evolution can affect their results. We would like to be transparent with the reader and admit that this section is by no means a complete list of all the reconstructions that have ever been produced, however, it does include the most well-recognized practitioners and reconstructions that are featured in scholarly publications, scientific textbooks, and on display at institutions of international repute.

The best documented 3D hominin reconstructions based on scientific methods were produced by the Russian anthropologist and archeologist Mikhail Gerasimov (Gerasimov, 1971). Gerasimov is especially renowned for his contributions to the field of forensic facial reconstruction—now more commonly referred to as facial approximation—which is the process of reproducing a likeness that can assist in identifying an individual from a skull found in a forensic context. In his published work, Gerasimov used his forensic methods—for a review of these methods, see Ullrich and Stephan (2016)—to reconstruct two Australopithecines as well as various members of the genus *Homo*. The best known 3D reconstructions of hominins today are produced by John Gurche (Balter, 2009; Gurche, 2013). Gurche has allegedly reconstructed over fifteen hominin individuals that are featured in the Smithsonian National Museum of Natural History in Washington, D.C. These reconstructions include *Sahelanthropus tchadensis*, *Australopithecus afarensis*, *Australopithecus africanus,* and *Paranthropus boisei*. Gurche has also reconstructed individuals from the genus *Homo*, including *Homo erectus, Homo heidelbergensis*, a Neandertal, and LB1 (Balter, 2009; Gurche, 2013). Other well-known practitioners of 3D reconstruction include Élizabeth Daynès, Gary Sawyer, Viktor Deak, Philippe Froesch, and Adrie and Alfons Kennis (Balter, 2009).

Is it important to note here that not all reconstructions of hominins have been produced in 3D since 2D reconstructions are arguably more numerous and thus any review would be incomplete without acknowledging them. In general, 2D reconstructions appear to conform less to the scientific approach and more to artistic intuition but this fact does not weaken their power of influence on public perceptions about human evolution and are therefore relevant to this review. Zdeněk Burian is one of the most celebrated 2D paleoartists in physical anthropology and produced a number of illustrations of hominins depicted in their ancestral environments (Jelínek, 1975). Jay Matternes also produced 2D reconstructions. One of these illustrations is of an individual of *Australopithecus afarensis* and is regarded by world-renowned paleoanthropologist Donald Johanson—who was consulted during the production of this reconstruction—as one of the “finest representations of this species” (Johanson, 1981). With respect to Burian, little is known regarding how the soft tissues were extrapolated from the fragmentary fossils upon which his reconstructions were based. Here we can only assume that these illustrations were reconstructed intuitively. In contrast to Burian, Matternes provides a full description of his methods. The reconstruction, he says, was made over an image of a composite reconstruction of an *Australopithecus afarensis* skull (Kimbel et al., 1984; Kimbel and White, 1988). The masticatory muscles and muscles of expression were constructed over the skull first, then existing methods for approximating the other features of the face were borrowed from the facial approximation literature, including mouth width determination, locating the eyeballs within the eye sockets, as well as deciding on the ear morphology, flexure wrinkles, and hirsuteness (Johanson, 1981).

Anyone attempting to reconstruct a hominin ought to be aware of the aforementioned practitioners and their influence on the current state of the practice. Scientists like Gerasimov and artists like Burian were some of the first to attempt to produce a hominin face from skeletal remains. Their results have functioned as hypotheses for the facial appearances of their subjects and while not all of these hypotheses may appear equally valid to the reader, we would like to propose that in the absence of a well-established systematic approach for reconstructing hominin soft tissues, these works provide valuable insights into each practitioners’ methodology. However, although these works have helped immensely in encouraging interest in human evolution, the methods employed by the aforementioned practitioners remain largely unchanged today. Gerasimov's methods have seen no improvement in their application to hominins and Burian's artistic intuition has been replicated by other artists, such as the paleoartist Mauricio Antón, with varying results.

THE PROBLEM OF VARIABILITY

Differences among hominin reconstructions were first systematically documented in a pivotal study by Karen Anderson, in which 860 hominin reconstructions were assessed from 55 museum displays across Europe and Australia. Inconsistencies between reconstructions of the same individual were found in both their surface appearances and body proportions (Anderson, 2011). To make matters worse, most hominin reconstructions were found to be presented without any rigorous empirical justifications. Despite this, and to the surprise of the authors, the same reconstructions are commonly cited in the scientific literature and presented in scientific textbooks on human evolution (Jelínek, 1975; Balter, 2009; Jablonski, 2013; Roberts, 2018). So severe are the differences between reconstructions of the same individual that it is almost as though the practitioners had never encountered another hominin reconstruction before commencing their own. From a scientific point of view, there are only two ways of explaining an error of this magnitude: either (1) the reconstructions are purely artistic interpretations based on individually constructed knowledge about human evolution, which can vary between practitioners and ultimately results in variability, and/or (2) the practitioners were using unreliable reconstruction methods. Why such varying reconstructions continue to be used in the dissemination of science when such reconstructions have never been formally verified is disconcerting to us because the quality of knowledge perpetuated by their use is clearly inconsistent. To make matters worse, consider the reconstruction of Lucy presented at the "Answers in Genesis" ministry's Creation Museum in Petersburg, Kentucky. While Lucy was indeed a primate, the decision to reconstruct this specimen as a knuckle-walker is an obvious error. However, the argument of variability put forward by the Creation Museum is a valid one that has, as of yet, not been addressed by the scientific community.

To the knowledge of the authors, Gerasimov is the only practitioner to express doubt about the use of his methods for reconstructing the faces of ancient hominins. He acknowledged from the outset that there was an inherent risk in interpolating soft tissue depth data collected from orangutans into his reconstruction of the *Australopithecus africanus* specimen Sts 5 (Gerasimov, 1971). In contrast, Gurche is on record saying that he developed his method for reconstructing hominins from personal research carrying out dissections of extant apes and modern humans (Gurche, 2013), but this research has never been formally verified nor published in any scientific literature. Regarding Élizabeth Daynès, Gary Sawyer, Viktor Deak, and Adrie and Alfons Kennis, none of these practitioners have ever published any details regarding their methods or justifying their results. Thus, at present it is evident that hominin reconstruction is a practice lacking a robust scientific and empirical foundation.

METHODS AND TECHNIQUES USED FOR RECONSTRUCTING HOMININS

To explore the question of why the aforementioned variability has and is still occurring, we will evaluate the evidence and methods available to practitioners of hominin reconstruction. As stated in the Introduction, to aid in our review we will present the various reconstructions performed by RC and GV over the last 6 years as case studies to (1) exemplify the quality of evidence that is available in each case and (2) to show what existing methods were employed in each case to explore their strengths and weaknesses.

Reconstructing Hard Tissues

The production of hominin reconstructions is interconnected with the discovery of fossils. This is not surprising since the internal skeleton serves as the basis for all of the external soft tissues. The vast majority of hominin fossils are represented by skulls, which are well-connected sets of bones that are usually preserved together, although often distorted or missing mandibles, unlike postcranial remains that consist of many separate bones that can become easily scattered in the environment (Suzuki and Takai, 1970; Sartono, 1972; Brown et al., 1985; Suwa et al., 2009; Berger et al., 2010; Kimbel and Rak, 2010; Laird et al., 2017). Postcranial fossils, by comparison, are exceptionally fragmented. Large portions of these fossils are poorly represented and/or were never recovered. Therefore, before the soft tissues for any hominin can be considered, the osteological material must first be reconstructed.

Methods for the reconstruction of hominin crania have been, and are still being, developed (Kimbel et al., 1984; Kimbel and White, 1988; Zollikofer et al., 2005; Gunz et al., 2009; Suwa et al., 2009; Kimbel and Rak, 2010; Benazzi et al., 2011; Amano et al., 2015; Brassey et al., 2018). In 1984, Kimbel, White, and Johanson reconstructed a male *Australopithecus afarensis* skull. The skull was a composite reconstruction that incorporated the skeletal elements from 12 different supposedly male fossil specimens found from sediments at A.L. 200-1a and one specimen found at A.L. 333/333w. This skull was later revised after the discovery of further fossil evidence (Kimbel and White, 1988). Similarly, in 1996, Tattersal and Sawyer revised Weidernreich and Swan's 1937 reconstruction of the skull of *Homo erectus* from a collection of casts from Zhoukoudian, China (Tattersall and Sawyer, 1996). This reconstruction was different from the Weidenreich and Swann skull, which was reconstructed as a female, whereas Tattersal and Sawyer reconstructed the skull as a male (Tattersall and Sawyer, 1996). To the knowledge of the authors, these are two of the only physical reconstructions of hominin skulls that have had their initial reconstruction and subsequent revision formally published. What this means for all other reconstructions of hominin skulls is unclear.

Reconstructions of hominin skulls facilitated by computer software are becoming increasingly popular (Gunz et al., 2009; Benazzi et al., 2011; Gunz and Mitteroecker, 2013; Kikuchi and Ogihara, 2013; Amano et al., 2015; Senck et al., 2015; Mounier and Mirazón Lahr, 2016). Gunz et al. (2009) produced virtual reconstructions of three hominin skulls from CT scans of the original specimens. These were the Taung child skull, the adult specimen of *Australopithecus africanus* Sts 5 (Broom, 1947), and a skull of the *Homo erectus* juvenile specimen KNM-WT 15000 (Brown et al., 1985). For the Sts 5 specimen, CT scans were combined with geometric morphometric methods to produce a complete skull. Landmarks were applied to a modern human cranium for the purpose of extracting coordinates and to produce a reference surface. The surface of the original Sts 5 cranium was then warped to match those coordinates taken from the modern human reference. This method goes beyond the reassembly of missing fragments like a jigsaw puzzle, such as those mentioned previously, as the entire fossil is replaced with a warped model of the modern human reference cranium. In other words, no fragments belonging to the original fossil are preserved in the result. For this reason, the method has received criticism (Senck et al., 2015). Accuracy of the method hinges on the correct use of reference surfaces. Interspecies and intraspecies reference surfaces can produce different results. Senck et al. (2015) concluded that it is possible to reconstruct hominin crania using reference surfaces but only if the morphometry of the subject being reconstructed is similar, or if bilateral symmetry can be exploited.

When we reconstructed the Taung child's skull in 2017, we used traditional molding and casting methods to produce a duplicate cast made directly from the first-order cast of the original specimen that was gifted to MH in 1995, rather than commercially available products—such as those from Bone Clones, Inc.—which are not exact copies of the original fossils themselves. The Taung fossil required very little restoration since its preserved parts provided enough anatomical constraints, such as occlusion and articulation, which meant that very few assumptions were needed to obtain complete anatomical information. However, in our reconstruction of Lucy's skull shown in **Figure 1C**, the reconstruction process was not as straightforward. Lucy, being the adult female specimen of *Australopithecus afarensis* and one of the most complete Pliocene hominin fossil skeletons ever found, has been subject to the facial reconstruction procedure more so than any other fossil hominin. By attempting to reconstruct Lucy's skull ourselves, we found that this specimen is a poor candidate for the facial reconstruction procedure because most of Lucy's cranial bones are missing. Lucy's mandible (**Figure 1B**) is relatively well-preserved and as such formed the basis for our reconstruction, but the cranium had to be digitally interpolated from the previously discussed composite male skull shown in **Figure 1A** (Kimbel et al., 1984; Kimbel and White, 1988). While doing so we discovered that the male cranium is much larger and does not articulate with the mandible well, so we scaled the cranium uniformly on all axes to fit Lucy's mandible based on bilateral symmetry and parabolic curve alignment of the upper and lower dental arches. The method we employed can be described as a "best-fit" approach and we do *not* by any means present our own reconstruction of Lucy's skull as the definitive version of this individual. However, it does show how each practitioner is required to model their own skull or borrow commercially available products that have never been formally verified.

What can be inferred from the methods involved in the reconstruction of hominin skulls is that separate methods are likely to produce varying results, especially in the case of Lucy. There is one other fact that needs to be acknowledged here. Since Lucy was discovered, other skulls have been found. So well-preserved are these skulls that almost no osteological reconstruction is necessary. The skulls belonging to individuals attributed to *Homo naledi* (LES1)*, Australopithecus sediba* (MH1), and *Homo floresiensis* (LB1) are just a few specimens that are ideal candidates for the facial reconstruction procedure (Brown et al., 2004; Berger et al., 2010; Laird et al., 2017). Despite these new discoveries, and to our surprise, there are still

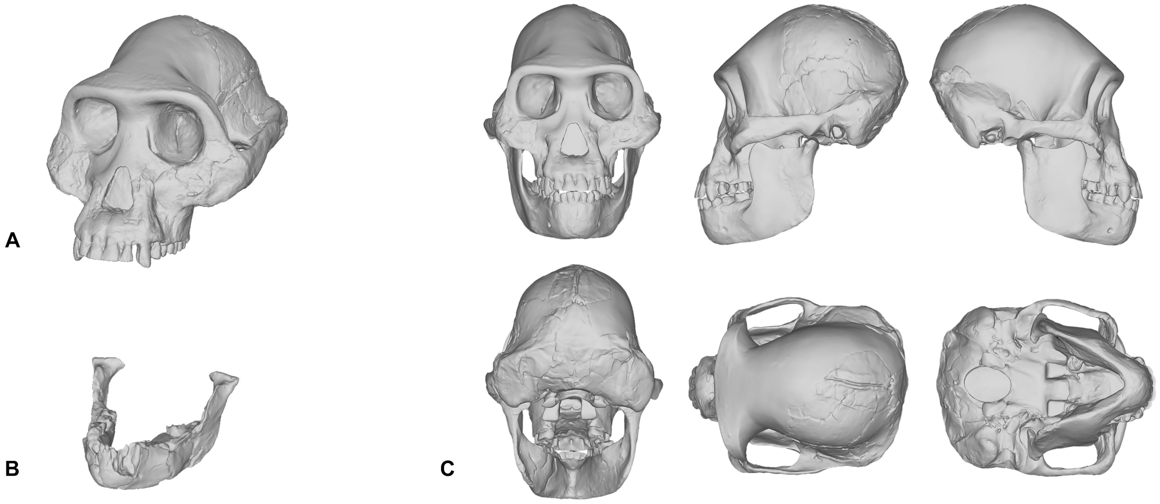

FIGURE 1 | Digital model of the *Australopithecus afarensis* composite male cranium reconstructed in Kimbel et al. (1984) and Kimbel and White (1988) **(A)**. Mandible belonging to the A.L. 288-1 (Lucy) partial skeleton **(B)**. Reconstruction of Lucy's skull that was produced by scaling the male cranium to fit the A.L. 288-1 mandible **(C)**.

facial reconstructions of Lucy being performed today. For these reasons, we would like to encourage practitioners to perform facial reconstructions on well-preserved fossils first before attempting to reconstruct those that are heavily fragmented.

Since this special issue is about more than just reconstructions of the skull and face, we feel that it is essential to include the various attempts at reconstructing hominin post-cranial skeletons in this review. However, an extensive survey of the scientific literature revealed that there is only one peer-reviewed article including a reconstruction of a complete hominin postcranial skeleton. The skeleton was reconstructed in a recent study exploring the use of a volumetric technique for estimating the body mass of hominins, in which a complete virtual 3D model was reconstructed for, yet again, Lucy (Brassey et al., 2018). However, in this case the subject is a logical choice since Lucy's post-cranial skeleton is exceptionally preserved. In this reconstruction, scans were made from casts of the original fossil bones and then virtual reproductions were articulated in computer software. 3D modeling techniques, such as mirroring and sculpting, were then used to reproduce existing parts of the skeleton. Additional hominin fossils were used for the completion of missing parts, including, but not limited to, an *Australopithecus sediba* (UW88-38) right clavicle and the *Homo habilis* specimen OH-8. Scans were also made from these elements and the virtual reproductions were then scaled to fit the partial skeleton. The thorax morphology was reconstructed using an iterative, geometric morphometric technique based upon a sample of both *Homo sapiens* and *Pan troglodytes*. The resulting 3D model of Lucy's skeleton was used in our reconstruction of Lucy's face and body (**Figure 2**). Putting the soft tissues aside for the moment to focus on the skeleton alone, we are not confident that the 3D model reconstructed in Brassey et al. (2018) is a true representation of Lucy's anatomy. The decision to reconstruct Lucy as an upright, free-standing hominin fully capable of erect bipedalism is well supported; it is indicated by the anatomy of the A.L. 288-1 fossil, the discovery of earlier and more numerous fossils attributed to *Australopithecus afarensis*, and the footprints from the Laetoli Beds of northern Tanzania (Leakey and Hay, 1979; Leakey, 1981; Johanson et al., 1982; Kimbel et al., 1984; Aiello and Dean, 1990). The footprints, for example, demonstrate that at the time of the *Australopithecus* there existed upright, free-standing hominins fully capable of walking bipedally and, therefore, Lucy has been reconstructed in such a way as to make this functionally possible. However, we agree with Brassey et al. (2018) in that the reconstruction is incorrect but only to the extent that the addition of skeletal elements from other specimens—belonging to separate species—will inevitably produce error, and how could it not? One could never confidently extrapolate the missing bones from an anatomically modern human with those belonging to a chimpanzee, so why would the talus from the *Homo habilis* specimen OH-8 be a suitable substitute for the talus of *Australopithecus afarensis*? We would also like to add that the ribcage is highly speculative. It is currently held that anatomically modern humans and hylobatids (gibbons and siamangs) share a barrel-shaped ribcage, whereas the great apes share a funnel-shaped rib cage. However, hypotheses about the shape of the *Australopithecus* rib cage vary and a consensus is yet to be reached on whether *Australopithecus* were markedly different from great apes and more similar to modern humans, or if the *Australopithecus* rib cage was more comparable to extant intermediates, such as hylobatids and orangutans (Bastir et al., 2017). Furthermore, the general stance of the skeleton is also potentially in error in part due to the ilium of the pelvis seeming to be angled in a position not seen in any extant hominin, much less a hominid. This horizontal position of the pelvis makes Lucy's stature shorter since the acetabula are raised upward and forward. Thus, similar to what has been previously discussed regarding hominin skulls, variability among post-cranial soft tissues is not just the result of differences in the shaping of the external appearances, it also appears to be the result of differences in the anthropometrics and arrangement of the underlying post-cranial skeletons.

FIGURE 2 | An intuitive reconstruction of Lucy's soft tissues (without hair and pigment) produced in 2018 and reconstructed over the digitally reconstructed A.L. 288-1 skeleton published in Brassey et al. (2018).

Although peer-reviewed articles including reconstructions of postcranial hominin skeletons are lacking in the scientific literature, there have been a number of reconstructions produced and published in books intended for a general audience. For example, in 2013 the skeleton of the *Paranthropus boisei* specimen OH5 was reconstructed by John Gurche for a display at the Smithsonian Museum of Natural History, and is featured in Gurche's (2013) book *Shaping Humanity*. The height of the skeleton appears to have been informed by a regression model developed in Gidna and Domínguez-Rodrigo (2013) and used by

Domínguez-Rodrigo et al. (2013) to produce minimum stature of 156 cm for this individual. However, the prediction model was developed using anatomically modern human anatomy, which Domínguez-Rodrigo et al. (2013) concede may not be appropriate in the case of the *Paranthropus* genus. We would like to highlight that even if the predicted minimum stature was correct, it does not provide the actual height for this individual nor the measurements of specific lengths of long bones. As of today, the only postcranial fossil that has been assigned to this species is the proximal end of an adult left femur. No other postcranial fossils have been confidently assigned to this species. Gurche provides a brief description for how he extrapolated the body from other australopithecine specimens (Gurche, 2013), but the results are highly speculative and virtually impossible to verify without the discovery of postcranial fossils belonging to *Paranthropus boisei*. The fact is that this reconstruction of *Paranthropus boisei* really only acts as an ill-informed hypothesis that is largely untestable. This is a notion that not only pertains to skeletal reconstructions of this species but to the practice of hominin reconstruction as a whole. What this rather obviously shows is that we are in desperate need of more fossil evidence, especially since bones serve as the starting point in all reconstructions of ancient primates.

Reconstructing Soft Tissues

Fossilized specimens of soft tissue are exceptionally rare. To the knowledge of the authors only one has ever been found for a primate (Franzen et al., 2009; Lingham-Soliar and Plodowski, 2010). The discovery was described as *Darwinius masillae*, an Eocene primate that lived 47 million years ago. What is most exceptional about this specimen is the almost complete skeleton, which is surrounded by a dark shadow representing the outline of the body and clearly showing gross anatomical details, such as the size of muscles surrounding the long bones, as well as minute details, such as the size of the external ears. Fossilized soft tissues have been found for other species, such as a specimen of the Cretaceous dinosaur, *Psittacosaurus* (Lingham-Soliar and Plodowski, 2010), and the Pliocene vulture, *Gyps fulvus* (Iurino et al., 2014). However, no such material has ever been found for any Plio-Pleistocene hominin species and, given the absence of soft tissue in the fossil record, there is no direct evidence for practitioners to extrapolate the soft tissues from or to compare their results with. Practitioners of facial reconstruction must therefore employ methods developed in studies of anatomically modern humans, which have mainly focused on the face. The foundations for these methods were laid in the nineteenth century by anatomists Hermann Welcker and Wilhelm His (Welcker, 1883; His, 1895). Welcker and His carried out the first documented research on the relationship between skull morphology and the soft tissues of the face by collecting soft tissue depths measurements at nine facial points from European cadavers, of which 37 were male and four female. A facial reconstruction was subsequently performed on a plaster cast of the skull of German composer and musician Johann Sebastian Bach using the measured thicknesses to construct the tissues of the face. This work has been often cited as one of the first facial reconstructions (Prag and Neave, 1997). Another well-known early facial reconstruction was performed by Kollman and Büchly (1898). Kollman and Büchly reconstructed the face of a Neolithic woman from Auvernier in Switzerland. The reconstruction was a joint effort, where Kollman collected soft tissue measurements from hundreds of female cadavers and produced a plan for the procedure and Büchly modeled the tissues onto the skull to produce the face. These early attempts of reconstructing faces to approximate the appearance of the deceased are cited in almost all of the literature on forensic facial reconstruction (Prag and Neave, 1997; Wilkinson, 2004).

Today, methods detailing the reconstruction process of the face are ubiquitous in the facial approximation literature (Stephan, 2003a,b,c; Stephan et al., 2003, 2013; Wilkinson, 2004; Hanebrink, 2006; Stephan and Simpson, 2008; Guyomarc'h et al., 2012; Richmond, 2015). Part of the challenge for any practitioner of hominin facial reconstruction is deciding which methods to use since a single anatomical feature may be reconstructed using a number of separate methods. In reconstructing the soft tissues of hominins faces, measurements at various cephalometric landmarks on the face must be determined. There are currently only three methods available to practitioners for reconstructing hominin soft tissues: (1) the thicknesses can be derived from mean values taken from measurements of modern humans—the best resource for deriving mean values comes from a recent meta-analysis of all the data drawn from across all of the literature (Stephan, 2017)—(2) the thicknesses can be derived from regression models developed from measurements of modern human skeletons and corresponding soft tissues, or (3) the thicknesses can be derived from mean values taken from measurements of great apes (chimpanzees, gorillas, and orangutans).

There are a few recognized reasons why mean values derived from either modern humans or apes, especially chimpanzees, may not be appropriate for reconstructing the face of Plio-Pleistocene hominins. First, means only express averages and thus do not represent the reality of individual variation within populations and, in fact, they completely ignore it. Furthermore, extrapolation of modern human depth data to archaic hominin skulls like those belonging to robust *Australopithecus*, such as the OH5 specimen, is predicated on the assumption that soft tissues depths between separate hominin species are identical, which is false based on what soft tissue measurements have been taken from chimpanzees (Hanebrink, 2006), and while extrapolation of mean chimpanzee values may produce less error than those for modern humans, very few measurements have ever been obtained for chimpanzees and therefore much of the face is still subject to artistic interpretation. For the above reasons, we rejected the use of averages in our own reconstructions. Conversely, the use of equations for predicting facial tissue thicknesses from craniometric measurements is gaining traction (Sutton, 1969; Simpson and Henneberg, 2002; Dinh et al., 2011; Stephan and Sievwright, 2018). Multiple significant correlations have been identified in samples of modern humans and regression models have been produced. As such, craniometric measurements of the skull can be used to produce facial tissue depths from regression models alone. Given that the soft tissues are tailored to each skull and are based on the verified relationships between soft tissue and craniometric dimensions, this method ought to be explored further, especially in great ape material, for the possibility of producing a set of regression models that have inter-species compatibility could reduce most of the variability between facial reconstructions of the same individual.

In our own experiments, results varied depending on whether intuition or equations were used. Given that practitioners of hominin reconstruction have chosen not to publish their methods it is not possible to link methods to any given reconstruction for the sake of comparison, so here we can only analyze our own facial reconstructions as a means of exploring the strengths and weaknesses of each method. To do so, we point to our reconstructions of the Taung child. The first reconstruction was produced using GV's sculptural and anatomical intuition alone, while the second was produced a year later using the same method except under the supervision of MH. As can be seen in **Figure 3**, there are obvious differences in their appearance. If intuited reconstructions that are produced by the same practitioner can vary, in particular with input from outside sources, then one can see clearly why reconstructions of the same individual produced by separate practitioners could vary wildly from museum to museum.

There are also other aspects beyond soft tissue thicknesses at specific points on hominin skulls that affect the variability exhibited between reconstructions of the same individual. The placement of the eyeballs within the orbits, eyebrow position, mouth width, and ear size arguably have more of an impact on the appearance than soft tissues alone. Much like soft tissue thickness, these features have been either reconstructed intuitively or using methods derived from studies of anatomically modern humans and great apes. In Gurche's reconstruction of the *Australopithecus africanus* specimen Sts-5, Gurche reconstructed the mouth width based on measurements of *Pan troglodytes* (Gurche, 2013), and eyeball position based on an unspecified ratio described in the appendix of his publication. In our reconstruction of the Taung child, we found that if official methods were not followed the reconstruction could be made to appear in a number of different ways. The mouth of the reconstruction in **Figure 3A** appears more prognathic than the reconstruction shown in **Figure 3B**. The ears are also larger and the flexure wrinkles more pronounced, which is more akin to young bonobos than to modern humans. In hindsight, it appears a concerted effort may have been at play to depict the subject as more ape-man (A) in one case and more man-ape (B) in the other.

In an effort to move away from intuition, our second facial reconstruction of Lucy (**Figure 4**) used equations derived from regression analyses of anatomically modern humans (Simpson and Henneberg, 2002). As one can see, it differs in appearance from the earlier reconstruction of Lucy in **Figure 2**, which was done intuitively without empirical data. This reconstruction may be perceived as an improvement over the previous Lucy since an empirical method was used, however, we believe that this is not at all the case. We must be fully transparent in stating that a number of the predicted values produced by the regression model yielded negative results, i.e., tissue thicknesses below 0.0 mm. Since it is not possible for soft tissue to be negative or equal to zero, these landmarks were excluded from the reconstruction and instead were extrapolated from the nearest relative predicted value. This error is likely a result of extreme values of the

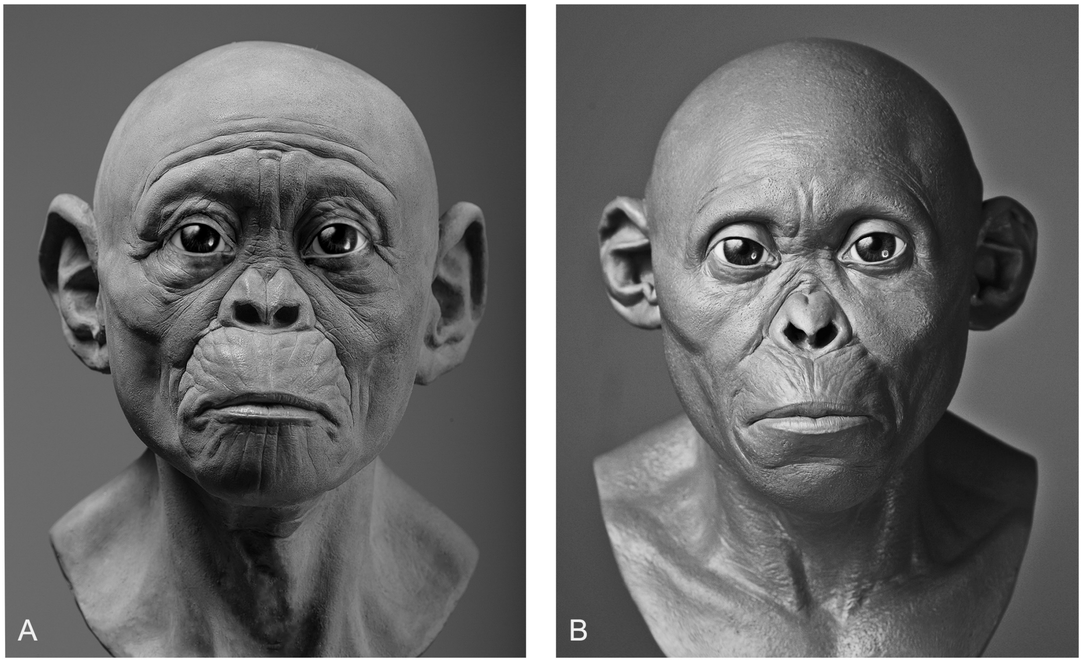

FIGURE 3 | Two facial reconstructions of the Taung child (without hair and pigment) that were produced one year apart. Please note how variability between these reconstructions is exemplified by the subjective decision to depict the subject as more apelike **(A)** or more humanlike **(B)**.

FIGURE 4 | A facial reconstruction of Lucy (without hair and pigment) produced in 2019 that employed facial soft tissue regression models developed in Simpson and Henneberg (2002) from modern human material.

independent variable. While some points did seem to conform to biological reality, based on mean comparisons, the fact that some points were entirely outside of possibility should cast doubt on the entire efficacy of human-derived regression models for reconstructing facial soft tissue in australopithecines. Thus, these equations are perhaps only appropriate for reconstructing hominins with craniometrics that are inside the normal range of variation observed in samples of anatomically modern humans.

Our reconstruction of the Neandertal specimen Amud 1 (**Figure 5**), for example, exhibits less of the aforementioned issues. The more proximal relationship of Neandertals to modern humans makes the use of the equations more viable. A number of other empirical methods derived from modern humans were also used, including positioning the eyeballs according to Guyomarc'h et al. (2012), the profile of the nose according to Prokopec and Ubelaker (2002), and the width of the mouth according to Stephan and Henneberg (2003). The final facial reconstruction of Amud 1 shown in **Figure 6** is similar to other reconstructions of Neandertals, especially in the size of the nose, suggesting that there is less variability in individuals that are compatible with existing methods of facial reconstruction derived from modern humans, although an explanation for this compatibility remains unclear. It is important to note here that while no values were reported as negative, unlike in our facial reconstruction of Lucy, we think the lack of lateral points on the skull offered by the equations resulted in too much intuition at these areas. This is because facial reconstruction methods have focused only on points of the face for the purposes of identification, whereas differences in the appearance between species can extend beyond the face to the whole head, like the temporalis muscles of OH5 for example. Thus, a more comprehensive study involving more measurements and points around the entire skull warrants further investigation.

Regarding soft tissue reconstructions of hominin bodies, the only published method we could find is described by Gurche (2013). This method, which has no empirical basis, was used to reconstruct the body of a number of Plio-Pleistocene hominins. We used the same method in our reconstruction of the body of Lucy in **Figure 2**. Like Gurche, we inferred the muscle proportions from comparative studies of fossil hominins and great apes. One of these studies reported that the ulnae of A.L. 288-1 have short, proximally oriented olecranons, whereas all great apes have long distally oriented olecranons (Drapeau, 2003). This difference in olecranon morphology is reported to be the result of different functional requirements. The long olecranons of the ape ulnae reflect powerful triceps brachii muscles adapted for arboreal use, whereas the short olecranons of A.L. 288-1 reflect triceps brachii muscles adapted for manipulative activities, such as tool making (Drapeau, 2003). Thus, in our reconstruction of Lucy's body, we reconstructed the upper limbs to reflect the functional predictions we could extrapolate from the ulnae. Unfortunately, comparative studies such as those described are lacking for the trunk and lower limbs, so these are highly speculative and subject to change. As a whole, we found that the intuitive method for reconstructing the soft tissues of hominin bodies far too imprecise.

Another point of contention is skin color, which is the single most under-researched feature in relation to hominin reconstruction and there is no known method for reliably reconstructing skin color in hominins. In modern humans, mass migration has made it impossible to predict skin color with any precision. This is mainly due to interbreeding and mismatches between the ancestral environments that shaped our appearance and the environments we inhabit now (Jablonski, 2013). This is perhaps the reason why no effort has been made to develop a method for reconstructing skin color in ancient hominins. The consequence of not having a method for determining the appearance of hominin skin is illustrated in the varying reconstructions produced by Gurche, Daynès, Sawyer, Deak, and the Kennis brothers, as well as in our own reconstructions. As can be seen in the completed facial reconstructions of Lucy (A) and the Taung child (B) presented in **Figure 7**, their skin tones differ significantly. We have interpreted this difference as a result of not having an empirical method for reliably reconstructing

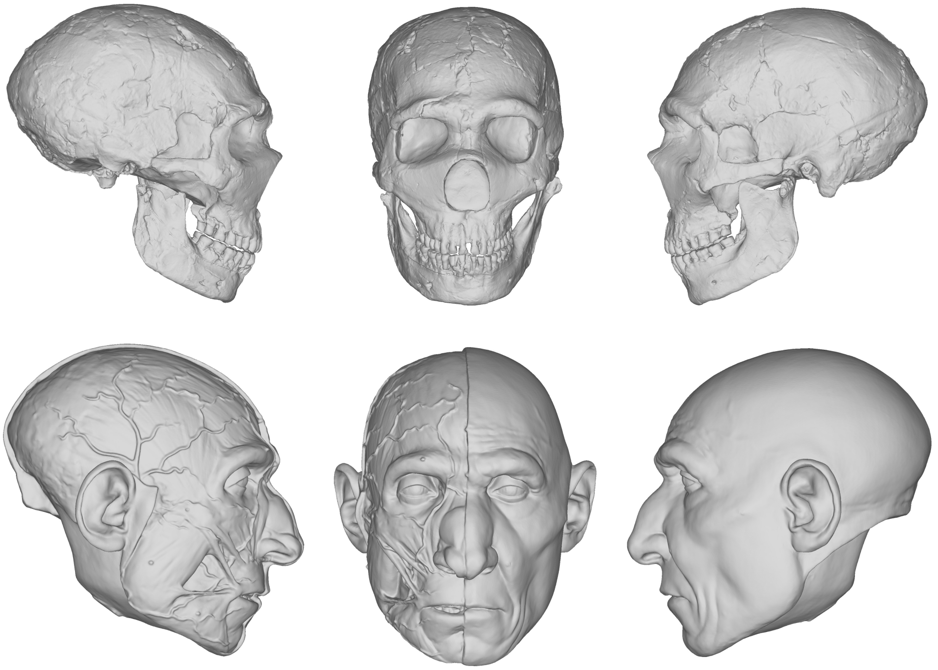

FIGURE 5 | Digital models showing the progression of the facial reconstruction procedure. Subject is based on a reconstruction of the Neanderthal Amud 1 cranium and associated mandible originally reconstructed by Suzuki and Takai (1970). Facial soft tissues were reconstructed using regression models developed in Simpson and Henneberg (2002) from modern human material.

epidermal melanin concentrations in australopithecines. The color of the Taung child's skin was reconstructed to appear similar to modern *Homo sapiens* native to Southern Africa. The decision to reconstruct the skin in this way is based on what is known about the function of epidermal melanin. Melanin evolved as a physical and chemical barrier to filter ultraviolet radiation. In humans there is a strong relationship between latitude and skin color and variation in skin color is the result of differences in concentrations of melanin (Blum, 1969; Relethford, 1998; Barsh, 2003; Chaplin, 2004; Jablonski, 2013). High concentrations of melanin are evolutionary advantages for populations in close proximity to the equator because it is the optimal arrangement for ultraviolet filtration in that environment. We assumed that for the Taung child to survive in Southern Africa there would have been no advantage in having low concentrations of melanin. Indeed, since it would have been a disadvantage and since ultraviolet radiation is the only known selective pressure for evolutionary change in melanin concentrations, we inferred that the skin of the Taung child would have been dark in appearance. However, even if this assumption is true, Lucy was reconstructed using exactly the same logic, although the results are very different. The appearance of the skin may be altered based on one's own subjective interpretation of the taxonomic position of these specimens. Both the African great apes, such as gorillas and chimpanzees, and modern humans have dark skin but "dark" is not nearly as descriptive as one may initially think. Regression models for reconstructing skin tone have been developed in Jablonski and Chaplin (2000), however, they measured melanin concentrations by skin reflectance, which does not provide the practitioner with a visual representation of the skin color of the subject. Research in this area offers the opportunity to present hominin populations with melanin concentrations that actually match their ancestral environments.

The color of primate pelage and differences between species further complicate the process of reconstructing surface appearance in hominins. For our reconstruction of Lucy and the Taung child presented in **Figure 7**, each hair was individually implanted into silicone casts of the reconstructions using a crown punching needle following the direction of hair in *Homo sapiens* and great apes described in Kidd (1903). We found that pelage was the most challenging feature to reconstruct because the pattern and distribution of hair cannot currently be extrapolated from bone alone. We tried to follow current hypotheses regarding thermoregulation via exploitation of exocrine sweating, which is often cited as a potential influence on the evolution of hairlessness in *Homo sapiens* (Wheeler, 1991, 1992), however, these hypotheses do not provide a current phenotype for specific species. Even considering further hypotheses about how hairlessness evolved from spending more time in aquatic environments (Hardy, 1960; Morgan, 1997), and in order to free our ancestors from external parasites (Pagel and Bodmer, 2003), neither of these explanations provided us with the specific instructions required to determine hair color and density. For all of these reasons, pelage poses a problem for museum displays. It has been said that baldness is preferable in an evidence-based reconstruction (Hayes et al., 2013). We do not necessarily agree with this as any reconstruction without hair may be perceived as incomplete or suggest that hominins did not have hair. This does

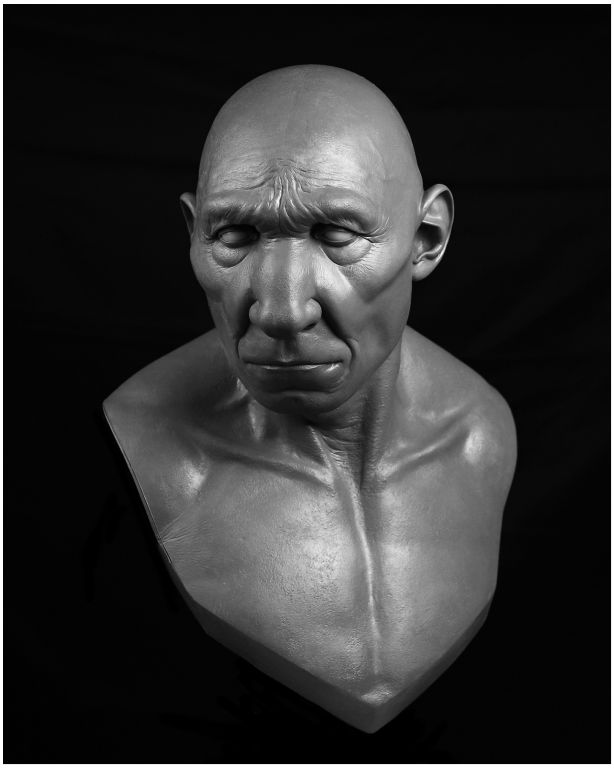

FIGURE 6 | Facial reconstruction of Amud 1 (without hair and pigment) produced in 2019 that employed facial soft tissue regression models developed in Simpson and Henneberg (2002) from modern human material.

not mean that we advocate for imaginary speculation in this area merely for the purpose of completing the reconstruction, rather, we would strongly encourage further research in this area.

FUTURE RESEARCH

The detection and analysis of DNA in extinct hominin finds is an emerging field and offers the exciting possibility of greatly enhancing reconstruction methods. Today, genetic research relevant to the practice includes the following: comparison between the genomes of *Pan troglodytes*, *Pan paniscus*, and *Homo sapiens* has revealed similarities between species and has enabled scientists to reconstruct the ancestry between them (Prüfer et al., 2012); the DNA of the Neandertals has been sequenced from a 38,000 year-old-fossil that was free from contamination with modern human DNA (Green et al., 2006), which has made it possible to compare the Neandertal genome to that of modern humans; and lastly, efforts to reconstruct the skeletal anatomy of the Denisovan's using DNA analysis generated body plans for these archaic hominins (Gokhman et al., 2019), as noted in the introduction, although the results are far from certain. Due to the chemical structure of DNA molecules, it is unlikely that they will preserve for more than several scores of thousands of years, thus there is little hope to obtain DNA of Pliocene/Early Pleistocene hominins. Proteomics seems to be able to study aminoacid sequences in ancient bones of greater antiquity since molecular structure of polypeptides preserves better than structure of DNA.

However, genetics does not currently provide the precise measurements needed for the reconstruction of both hominin soft tissues and underlying bone structures. The morphology of the bones in the illustration showing the Denisovans body plan is highly subjective (Gokhman et al., 2019). There is currently no known method for deriving anthropometric measurements from genomes, highlighting a major problem with the proposed body plan. The main purpose of the illustration appears to be providing an example rather than a precise depiction of anatomical forms from the past. Therefore, it seems that anatomical data are best provided by direct observations of anatomical structures. There is the possibility that genetic research will provide information about hominin appearances that cannot be determined from bone alone. Eye, hair, and skin color are just some aspects of hominin appearances that may be determined from the sequencing of ancient hominin genomes. Unfortunately, this information will be restricted to specimens from the late hominin record (Neandertals, Denisovans, and LB1) because, as stated, DNA extraction is not possible from fragments that are older than a few hundred thousand years. Worse still, DNA extraction from fossils is impossible. Fossils are bones that have all organic compounds replaced by minerals from soil and do not contain DNA. Alas, the only hominin remains that will be available for genetic research will be those that are not fossilized.

THE ETHICS OF RECONSTRUCTION AND SOCIETAL IMPLICATIONS

Given what Anderson (2011) has shown regarding the variability present in reconstructions of the same individual across separate museum displays, it is clear that very little effort has been made to produce reconstructions that are substantiated by strong empirical science. This is surprising given how museums boast about decades of success presenting scientific knowledge and education to the public. While in large part this is true and they provide an invaluable service to society, with respect to hominin reconstructions, they appear to exaggerate the methods used or this information is left out of their displays entirely. The reasons for this are not certain so we can only hypothesize as to the reasons why. It can most likely be attributed to factors outside the control of science, namely economic and social concerns. The immense pressure for museums to produce exhibits that are exciting may get in the way of any efforts to present reconstructions that are based on actual scientific knowledge, which requires time and effort. Exciting exhibits that feature large and very complete objects may attract non-traditional audiences, whereas small exhibits that grow over time presenting what is actually known about the appearance of Plio-Pleistocene hominins may only be of interest to a narrow audience.

Museums are often hubs for scientists and educators to share ideas with each other and find practices to excite the public with their enthusiasm. Truly, despite our criticisms, we acknowledge that generations of learners of all ages, educators, artists, and all forms of curious people have benefited greatly

FIGURE 7 | Pigmented silicone casts of facial reconstructions of Lucy **(A)** and the Taung child **(B)** showing different skin tones. Lucy's tone has been reconstructed to appear more similar to that of bonobos, whereas the Taung child's tone is more similar to that of anatomically modern humans native to South Africa.

from the existence of museums. However, presenting information that is not known diminishes the value of that which *is* known and may lead to confusion and discourage further interest in human evolutionary theory. There are potential educational harms in presenting unscientific reconstructions of hominins under the shroud of presumed validity. Therefore, with the cultural role of a museum and any educational institution, or any educational tool at all, comes an added responsibility to take pains to avoid accidentally, or worse, willfully misinforming the public.

While institutions showcasing and not challenging these empirical errors is troubling, other errors less concerned with what hominins looked like can be potentially far more damaging to social perceptions of evolution and its implications. To explore this point, it is important to introduce a couple of terms and a sentiment from an artistic perspective. For the academic art community, understanding iconography and iconology when creating representational works is crucial. In the visual arts, iconography is the study of subject matter itself and iconology is an attempt to analyze the significance of that subject matter in relation to the culture and individuals that produced it. This distinction is important because depictions of hominins do not exist in a vacuum, rather they are seated in the historical contexts of not just science but also those of the arts and cultures. This issue has been discussed in many books, including Moser's (1996) *Ancestral images: the iconography of human origins*, which analyzes how biases, prejudices, and stereotypes had been crucial in such reconstructions and further reinforced by them. Therefore, like an institution can be held accountable for what it promotes and showcases to the public, artists too can be held accountable for how they represent their subjects in their artworks.

In Van Laar and Diepeveen (1998) the roles artists function under within society are explored. One of these roles is that of the artist as an intellectual. This role is exemplified as the artist who deals with areas of human knowledge and contributes to them; the paradigmatic career of Leonardo Da Vinci comes to mind as the example that fits this mold. The tradition of artists working within the disciplines of science has undoubtedly contributed to scientific knowledge. As such, it can easily be argued that artists working in the field of hominin reconstruction operate under a similar role. However, as Laar and Diepeveen point out, with the obvious benefits to this role comes the danger of elitism being exercised by the artist. Artists tend to get self-absorbed in their claims about art and culture, making artwork that is seldom understood by the public and often disagreed with by art professionals. In other words, what begins with a sincere interest to contribute to human knowledge can become an ideological arms race in a competitive art field regarding the insights of individual artists who constantly jostle for artistic relevance. While this point is being made within the context of the art world, this same danger is present in the field of hominin reconstruction. Artists who are commissioned to sculpt models for museums tend to be highly skilled in the sculptural arts and their interest to contribute to science is at times overshadowed by what they can do artistically. Like the ideological arms races of heady conceptual artists, the museum display circuits can also be subjected to a similar form of competition. They can be so much more concerned with making science exciting that they can forget the underlying mission of their role in this context, which is to disseminate and contribute to actual scientific knowledge. Artists who purport to facilitate the dissemination of scientific material, whose works are also hosted by renowned institutions of learning, are understandably perceived by the public as experts in their field. However, when artists operating as disseminators of science fail to make sure their models showcase the best available evidence, they fall short in their role of not just educators but artists as well. When work is being consumed by the public for scientific understanding, that status comes with immense responsibility and accountability. Throughout history, people of all ages have looked to artists for inspiration, contemplation, and in many cases like the ones in question, information. Artists who do not take into account or even exploit their contextual roles are at risk of doing society a disservice.

For example, consider the most iconic image of human evolution: Rudolf Zallinger's The March of Progress, also known as The Road to *Homo sapiens*. Gould (1989) was the first to point out the flaws in this reconstruction, which perpetuates a number of misleading, and potentially harmful, ideas about human evolution. First, it presents the erroneous view that evolution entails a linear progression from animal to ape, to ape-man to the so-called "Negroid race" and then to the "Caucasoid race." This Euro-centric bias not only makes biological errors but also projects ethical insensitivities. Note that the Zallinger's image was printed in a series of Science books for public consumption in America in 1965 at the height of the civil rights movement in a country wherein people were afforded different sets of rights and often denied basic freedoms, all based upon variations in skin color. Based on the pernicious bias out of which this image was made, it is hardly appropriate to use it for disseminating scientific information about human evolution. However, imagery of this kind is still being used today. In a promotional video advertising Gurche's reconstructions present at the Smithsonian Museum of Natural History[1], the same errors are present. It shows a linear progression through evolutionary time, transitioning from one genus to the next from *Sahelanthropus tchadensis* to *Australopithecus* to *Homo erectus*, to *Homo heidelbergensis* to a Neandertal and then finally to *Homo sapiens* represented by a photo of Gurche himself, who is of European ancestry. Visual material of linear simplified progressions of this sort, even if accidental, can act as a tone-deaf reminder of the history of Europeans holding a place in academia dictating to minorities where they come from and often where they stand in this unscientific hierarchy. This is perhaps most easily seen in the history of art museums and natural history museums housing art in a segregated manner. As expressed in Stanish (2008), art museums have historically showcased the art of the European masters, whereas natural history museums housed the art of indigenous peoples. This Eurocentric myopia has the effect of alienating minorities by putting their artwork in the context of natural history; the domain where we observe the natural world as a separate entity from it. Conversely, the art museum is the domain of artistic achievement. The act of segregating minority culture's artworks to the building where we study animals is akin to only representing African bodies as a steppingstone on the progression of evolution behind the European body. It may not sound like a point of scientific relevance, but in the field of visual arts one's audience, content, and context are inextricably linked. Artists who show imagery that has relevance to the very identity of our species should be well versed in the troubling iconology surrounding these types of imagery. If education and dissemination are the aims of museums and textbooks, then an extra level of care should be employed in not just what we depict, but how they are depicted and an intimate understanding of who the audience is. Consider how young, would-be academics of minority groups feel as they are readily encountered by not just scientifically unsubstantiated material, but material that echoes a history of racist attitudes toward groups that look like them. One could understand how visual material of this sort can discourage interest in science.

It is important to note here that it is not the intention of the authors to discourage artistic expressions of scientific ideas. If anything, we whole-heartedly support such explorations. As previously noted, artists have held various roles in society and often operate as an inspirational force that can inspire new perspectives outside of the purview of more methodological domains like science. To expand on this point, an artwork by one of us (GV) is presented in **Figure 8**. Shown is a work inspired by the artist's involvement within the sciences while employing formal and conceptual cues from art history to explore ideas of identity, origin stories, and even use the formal elements of the veiled cloth as a metaphor for how much is yet to be unveiled about the appearances of our ancestors and evolutionary history as a whole. This work, and other artwork involving the depictions of scientific ideas and/or specimens, serve to invoke thoughts, emotions, and concepts that are of a socio-political and philosophical nature. Thus, works like this have domains in which they are more or less appropriate. Within the domain of the contemporary art gallery or art museum, the scientific inaccuracies or artistic choices are of little consequence since the context puts more weight on the work's philosophical implications. Conversely, picture for a moment this statue, labeled as an artistic rendition of Lucy, in a natural history museum. Unless there are clear plaques and context-giving aids revealing that the body and its proportions are speculative, and that the use of cloth is a conceptual artistic freedom, this statue would surely mislead adult and, especially, younger museum goers due to the museum-imposed context of education and trust. As the opportunity for confusion outweighs the possibility of education, the prospect of such a work in a natural history museum is perhaps an inappropriate context barring exceptional caveats. Yet, there may not be a need to draw such a dichotomous view; if the statue served as an entrance piece that primes the viewers to think about how much we do not yet know, and how heavily veiled the truths about our past are, it can begin a healthy dialogue about what the rest of this imagined exhibit may present to its visitors in the way of fossils and other remains. This is but one example of a way of an artistic object exercising artistic license can operate in an educational context. Yet, this kind of conceptual artistic license is not the one usually taken in museums of natural

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[1] https://www.youtube.com/watch?v=ru8ifph_q9o

FIGURE 8 | A marble sculpture titled "Santa Lucia" carved in 2019 following the body-composition of the intuitive reconstruction of Lucy previously shown in **Figure 2**.

history, instead practitioners of reconstructions take *scientific license* and create works much less founded on science than the museums prop them up to be. This is a case of a dim use of the word "art" and "license" operating as handwaving to simply allow artists to fill in the massive gaps in the available evidence with their "vision" without being honest with the public that they are engaged in highly speculative representation. The issue then becomes one of transparency, wherein exhibits could (and perhaps should) take care to show viewers the very exciting and wonderful facts we have uncovered and how much more we do not yet know. This would make what is shown in exhibits scientifically relevant and not inadvertently (or worse purposefully) making claims through their exhibits that are unfounded scientifically as previously discussed. Not taking full account of the context and role both the artist and museum serve together in the aims of scientific dissemination in society can have an adverse effect on the ability of these institutions to fulfill their self-stated aims of societal outreach and education.

Therefore, models, illustrations, and videos published by reputable institutions and trusted names like the Smithsonian Museum of Natural History should be held to a similar level of scrutiny as papers published in peer-reviewed journals. This is justified given the quantity of daily visits to museums around the world and the amount of visual consumption of content from museum displays, their websites, and printed material, which is far more accessible to the general public than any scientific article. For these reasons, scientists, artists, and museum curators involved in reconstructing our evolutionary antecedents must be very conscious of their role in society as arbiters of scientific facts and the consequences of not conforming tightly to this responsibility. These institutions are ones with a long history of community outreach which have no doubt touched many lives for the better, the authors included. These places have long served as a space where people come to learn and be exposed to not just science, but also to its questions and complexities. Where facts about hominin appearances are unknown, institutions can look to highlight the process of scientific discovery and be transparent instead of relying on artistic liberties and interpretations. Where interpretations or artistic speculation is undertaken, appropriate caveats and information should be readily offered until further research improves on these assumptions. While reconstructions currently displayed in museums globally are impressive for their technical achievement, their lack of scientific foundation paired with an overstatement of their scientific validity may undercut the trust of the public and betrays the very responsibility of dissemination that is expected from such spaces of potential learning.

CONCLUSION

The choice of hominins as a case study for this introductory paper of this special issue on muscle reconstructions is due to its value for broader discussions on such reconstructions and on both their ethics and societal implications. Muscle reconstructions are not only of interest to, and used by, scientists, rather they are used in art, textbooks, the press, social media, museums, schools, universities, and many other institutions. That said, the practice of hominin reconstruction has been mostly disregarded as a scientific activity and consequently has not been held to the same standard of scrutiny as peer-reviewed research, despite how the practice is currently perceived. The practice has essentially fallen into the hands of artists who, with no scientific framework of methods yet established for the reconstruction of Plio-Pleistocene hominins, performed the procedure however they wished. Some artists have relied mostly on their intuition regarding the soft tissues, while others have employed the use of forensic facial approximation methods generated from studies of modern human material. However, highlighting such complexities and difficulties also allows us to be aware of the fascinating opportunities that we face: it is a real opportunity for science to offer an alternative and to develop the practice of hominin reconstruction from one that is mostly an artistic activity to one that is a strong empirical science.

The question of whether the aforementioned is worth exploring in science seems to be mostly a matter of subjective opinion. Here, the authors would like to propose that no argument can be made against its exploration. Surely, if there is even the slightest evidence to suggest that the practice may improve, then exploration and growth in this area should be encouraged rather than dismissed. Hominin reconstructions are predominately used for the dissemination of scientific information to the public in museum displays and students in university courses, which will influence the way we perceive our common origins, our fellow human beings, and the way we perceive and define humanity more generally. Thus, biologically accurate reconstructions built upon strong scientific foundations will be a non-trivial improvement that will enhance their efficacy and have a positive impact on the public understanding of evolutionary science; a branch of science concerned with our own ancestors and history. This underscores our responsibility regarding their depiction and dissemination because regardless of whether it concerns apes, monkeys, earlier tetrapods, or earlier fish, they are all our evolutionary relatives in the ever-branching biological tree of life.

AUTHOR CONTRIBUTIONS

RC initiated the investigation into scientifically accurate hominin reconstructions, analyzed the literature, wrote the majority of the manuscript, and edited the whole version of the manuscript. GV wrote the section under the heading "The Ethics of Reconstruction and Societal Implications," carved the sculpture featured in **Figure 8**, modeled all reconstructions featured in **Figures 1–7** in partnership with RC, and edited the whole version of the manuscript. MH advised the reconstructions featured in **Figures 2–7**, was involved in the 6 year partnership reconstructing hominins with RC and GV, and edited the whole version of the manuscript. RD had the idea of doing this manuscript for this special issue, wrote the section under the heading "Introduction: Why Study and Reconstruct Muscles?", and edited the whole version of the manuscript. All authors contributed to the article and approved the submitted version.

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Chapter 3: The Soft Tissues

Towards the restoration of ancient hominid craniofacial anatomy:

Chimpanzee morphology reveals covariation between craniometrics and facial soft tissue thickness

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Context of Research Article

The incorporation of accurate facial soft tissue thickness measurements during the reconstruction procedure is paramount to reducing variability exhibited in reconstructions of the same individual. Within the facial approximation literature, means have received the most scientific attention. However, there is a recognized error in extrapolating means to individuals; means completely ignore the scientific fact of variation among individuals.

In an effort to circumvent this limitation, covariation between soft tissue and craniometric measurements has been explored. Correlations have been found and multiple regression models have been used to generate equations for improving estimations of soft tissue thickness from craniometrics in modern humans. However, such correlations have not yet been explored in great ape material.

The aims of this research were to (1) provide a facial soft tissue thickness dataset for adult chimpanzees, and (2) to provide a set of regression equations that can be used to reconstruct the facial soft tissues for very ancient hominids, such as those dated from 4.0 to 1.2 million years ago.

This article represents the first time that such a collection of tissue depth data has been collected and presented for chimpanzees in a systematic manner, as well as the first time that covariation has been identified in non-human material. This article also includes three hominid reconstructions produced using said covariations within its figures.

The soft tissue thickness data for chimpanzees are freely available for anyone to download on Figshare, as are cephalometric landmark reference charts for chimpanzees. Similarly, the equations, which resulted directly from this research, are also included within the tables and can be implemented in future practitioners' reconstructions. As such, I am positive about the utility of this research for future efforts reconstructing very ancient hominids, as well as for comparative studies within and outside the discipline of biological anthropology.

Statement of Authorship

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Overall percentage (%): 85%

Certification: This paper reports on original research I conducted during the period of my higher degree by research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.

Signature: ______ ______________________ **Date:** 10 / 09 / 2021

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. The candidate's stated contribution to the publication is accurate (as detailed above);
ii. Permission is granted for the candidate to include the publication in the thesis; and
iii. The sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author: Gabriel Vinas

Contribution to the paper: Gabriel Vinas prepared skulls for 3D printing, performed the 3D reconstructions presented in Figures 3 and 7, contributed to the conception and design of the project, interpreted research data, edited the manuscript, and approved the final version of the manuscript.

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Name of Co-Author: Maciej Henneberg

Contribution to the paper: Maciej Henneberg contributed to the conception and design of the project, interpreted research data, edited the manuscript, and approved the final version of the manuscript.

Signature: _____ ______________________ **Date:** 10 / 09 / 2021

PLOS ONE

RESEARCH ARTICLE

Towards the restoration of ancient hominid craniofacial anatomy: Chimpanzee morphology reveals covariation between craniometrics and facial soft tissue thickness

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Abstract

In modern humans, facial soft tissue thicknesses have been shown to covary with craniometric dimensions. However, to date it has not been confirmed whether these relationships are shared with non-human apes. In this study, we analyze these relationships in chimpanzees (*Pan troglodytes*) with the aim of producing regression models for approximating facial soft tissue thicknesses in Plio-Pleistocene hominids. Using CT scans of 19 subjects, 637 soft tissue, and 349 craniometric measurements, statistically significant multiple regression models were established for 26 points on the face and head. Examination of regression model validity resulted in minimal differences between observed and predicted soft tissue thickness values. Assessment of interspecies compatibility using a bonobo (*Pan paniscus*) and modern human subject resulted in minimal differences for the bonobo but large differences for the modern human. These results clearly show that (1) soft tissue thicknesses covary with craniometric dimensions in *P. troglodytes*, (2) confirms that such covariation is uniformly present in both extant *Homo* and *Pan* species, and (3) suggests that chimp-derived regression models have interspecies compatibility with hominids who have similar craniometric dimensions to *P. troglodytes*. As the craniometric dimensions of early hominids, such as South African australopithecines, are more similar to *P. troglodytes* than those of *H. sapiens*, chimpanzee-derived regression models may be used for approximating their craniofacial anatomy. It is hoped that the results of the present study and the reference dataset for facial soft tissue thicknesses of chimpanzees it provides will encourage further research into this topic.

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Introduction

The primate family of Hominidae is comprised of the African apes, humans and all ancestors leading to these clades. Reconstructing soft tissue characters of extinct members of the

Hominidae, called here hominids, has become an increasingly popular practice with many approximations of their faces presented in museum exhibitions, popular science publications, and at conference presentations worldwide [1–3]. In these contexts, reconstructions of the face and body have proven to be an effective vehicle for the dissemination of scientific information about human evolution. However, there is a recognized problem of variability among reconstructions of the same individual. A recent study comparing approximations of LB1, the holotype of *Homo floresiensis* [4, 5], reported that they vary significantly among one another [6]. Similarly, in a systematic survey of 860 hominid reconstructions presented in 71 museums across Australia and Europe, it was found that inconsistencies are prevalent in all other approximations of extinct hominid species [7]. If practitioners were using consistently reliable methods this variability would not have occurred. Obviously, the confounding effect of practitioner experience and competency in the reconstruction procedure also plays a role here. However, there is clearly variation in the replicability across existing reconstruction methods depending on the robustness of the empirical data supporting them and, since there is currently very little applicable data that can be extrapolated to Plio/Pleistocene hominids, results vary depending on methods used and individualities of practitioners.

Worse still, in its present state the practice of hominid reconstruction is particularly vulnerable to attack. Campbell et al. [8] argues that reconstructions based on unspecified sets of assumptions and biased misconceptions can actually do harm by perpetuating erroneous ideas about human evolution. Critics of human evolution are already using discrepancies between reconstructions of the same individual to undermine the reliability of evolutionary theory. Therefore, it is of utmost importance to strengthen methods of reconstruction as much as possible to reduce this variability and avoid such criticisms.

The term used to describe the process of building a face over a skull varies in the literature between disciplines. In forensics, the name of the process most commonly referred to as ‘facial reconstruction’ was updated to ‘facial approximation’ because it is a more accurate description of the results, whereas in paleoanthropology the term ‘facial reconstruction’ is still being used [2]. Regardless of what term is preferred, the results are always approximate and therefore we agree with previous authors and prefer the term ‘facial approximation’ [6, 9, 10]. Scientific testing of facial approximation methods has been a major focus in craniofacial identification of human remains with research dating back at least to Welcker [11], with important contributions by Gerasimov [12, 13], Prag and Neave [14], and Wilkinson [15]. Methods using means of soft tissues of the face have received the most attention [16–19], however, there is a recognized flaw in extrapolating means to individuals. As statistically robust as means may be, they only express means for specific populations. For reconstructing individuals, population means are not appropriate because they completely ignore variation among individuals. Regarding the approximation of extinct hominids, interspecies extrapolation of means derived from either modern humans or the extant great apes (*Gorilla*, *Pan*, and *Pongo*), as suggested in Hanebrink [18], is equally inappropriate because it also ignores variation among individuals.

One possible solution to this problem is to identify approximation methods that are compatible across all members of the Hominoidea superfamily. If a consistent pattern in covariation between soft tissue and craniometric measurements can be identified in extant hominids, then extinct hominids can reasonably be assumed to have followed suite. Such covariations were first explored in human material by Sutton [20] and extended in Simpson and Henneberg [21]. Correlations were found and multiple linear regression models were used to generate equations for improving estimations of soft tissue thickness from craniometrics alone in modern humans, though this covariance has rarely been used in facial approximations. Reactions to the results of these studies are mixed. Stephan and Sievwright [22], using data measured with substantial random errors, report that regression models have low correlation coefficients that do not improve soft tissue thickness estimates above population means. However, Dinh, Ma [23] repeated the use of linear regression models and produced favorable results that encourage further exploration. Thus, for the purpose of hominid facial approximation, the possibility of generating soft tissue thickness values that are individualized to a specific hominid specimen is undoubtably better than extrapolation of species-specific means.

The present study is motivated by the aforementioned concerns and while we hold that the findings reported here are valuable we raise three caveats at the outset: 1) As in previous studies of chimpanzee soft tissues [24–26], this study includes only a small sample of chimpanzees and, therefore, the conclusions from the results are subject to further testing on larger samples; 2) We also do not include other members of the African ape clade and so we cannot expand our findings to the entire Hominoidea superfamily; and 3) We do not claim to eliminate the need for informed speculation in hominid facial approximation entirely. Not all soft tissue characters of ancient hominids are addressed here, such as the facial features (eyes, nose, mouth, and ears), which arguably have a much greater impact on the variability between reconstructions of the same individual than soft tissue thicknesses alone. This work represents a step towards an empirical method that will strengthen the practice, but it is by no means a final solution to the problem.

The aims are: (1) To validate in chimpanzees (*Pan troglodytes*) that facial soft tissue thicknesses covary with craniometric dimensions, and (2) to produce soft tissue prediction models with interspecies compatibility from chimpanzee material that can be used in the facial approximation of extinct hominids.

Materials and methods

Computed tomography scans of 28 chimpanzees were collected from two separate data repositories. Scans were accessed online, via the Digital Morphology Museum, KUPRI (dmm.pri.kyoto-u.ac.jp) and Morphosource (https://www.morphosource.org), and obtained as Digital Imaging and Communications in Medicine (DICOM) format bitmap files. After excluding two neonates, one infant and six subjects showing obvious pathological effects or degradation caused by decomposition, the study sample contained 19 individuals of known age, sex, and subject condition. The sex ratio was 1:1.71 (7 male and 12 female) and the mean age was 30.9 years (minimum = 9; maximum = 44; SD = 10.1). Subject condition was varied and included seven living, five fresh, five frozen, and two subjects that were preserved by immersion. Information on whether individual subjects were scanned in the supine or prone position was not available at the time of this study. Further information on whether subjects had been living in the wild prior to scanning was also not available but the study sample is assumed to consist of animals that were housed in captivity only. A complete list of all subjects used in this study is presented in the (S1 Table).

Prior to measuring, all skulls were oriented in the Frankfurt horizontal plane determined according to its original definition by a horizontal line passing through the inferior border of the orbital rim (mid-infraorbital) and the top of the external auditory meatus (porion) on both sides of the skull. Facial soft tissue thickness was then measured at 39 cephalometric landmarks (Fig 1; 17 medial and 22 bilateral) in OsiriX, v. 11.02 (Visage Imaging GmbH, Sand Diego, USA), which has been shown to produce accurate measurements that can be reliably compared between separate studies [27, 28]. Cephalometric landmarks were selected based on common depths found in the facial approximation literature [21, 29–31]. However, to allow for other aspects of the head beyond the face to be investigated, further points were added to include a wider range of points than normal, particularly points on the lateral areas of the head. The decision to include additional points can be explained as follows. The purpose of facial

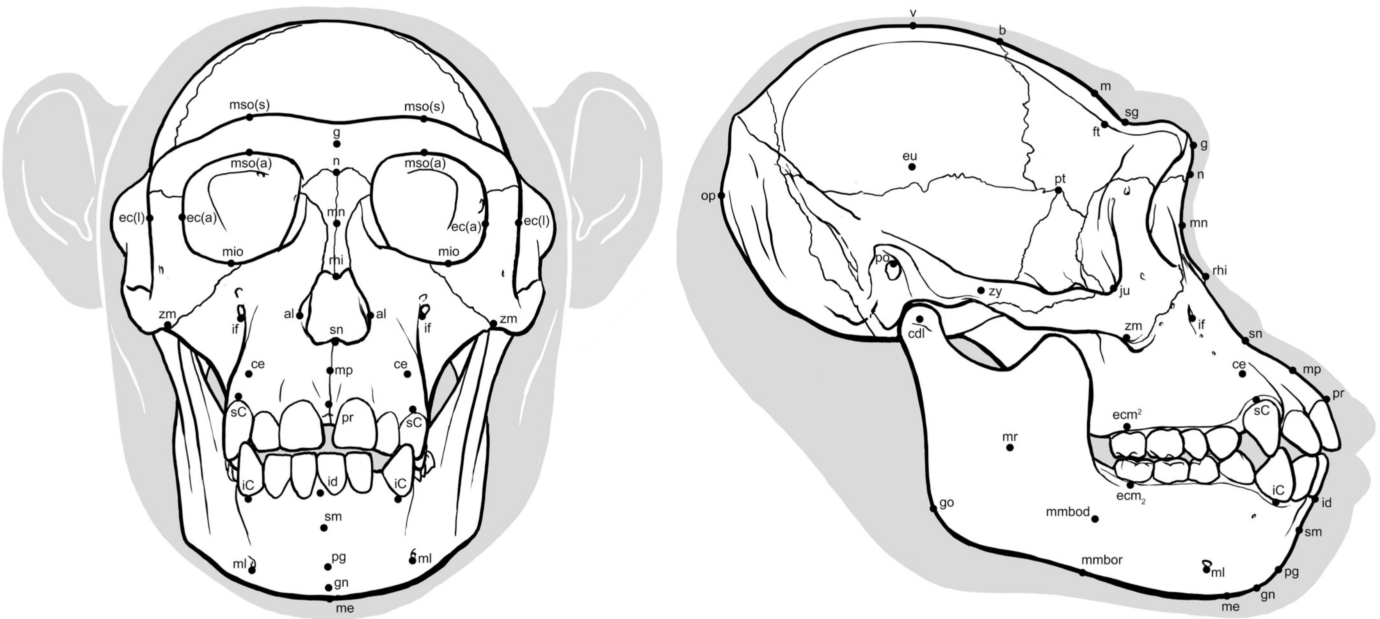

Fig 1. Locations of cephalometric landmarks on *Pan troglodytes* skull in norma frontalis and norma lateralis. See abbreviations in Table 1.

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approximation of modern humans is to generate a specific recognition of a target individual, however, in facial approximation of ancient hominids the purpose is to show morphological differences between separate species. As morphological differences extend beyond the face to the rest of the head, the inclusion of further points allows for such comparisons to be made. A maximum total of 61 soft tissue depth measurements were possible per individual as well as 21 measurements of craniometric dimensions. All cephalometric points were positioned onto 3D volume renderings of the skulls prior to measuring with the exception of 6 points (gnathion, metopion, mid-mandibular body, mid-mandibular border, mid-nasal, mid-philtrum) that were more precisely aligned in 3D multiplanar reformatting by halving the inter-landmark distance between two adjacent points along the sagittal plane. When analyzing scans, it was noticed that some sutures of the cranium had been obliterated. However, as sutures are needed for the positioning of bregma, dacryon, ectoconchion, nasion, pterion, and zygomaxillare, these points were positioned and cross-checked against a reference skull of a chimpanzee from the Vernon-Roberts Anatomy and Pathology Museum, University of Adelaide. Depths at all landmarks were then measured perpendicular to the bone surface using the coronal, sagittal, and transverse planes to control the direction of measurement. Xscope, v. 4.4.1 (ARTIS Software, Virginia, USA) was used to superimpose horizontal and vertical guides during the measurement procedure to keep measurements parallel to the reference planes. For thicknesses at bilateral landmarks, measurements were taken from both the right and the left side of the face and then the mean was calculated. Very few depths were unobtainable with the exception being those landmarks located in areas of incomplete DICOM data or where the soft tissues were outside of the anatomical position. For example, craniometrics crossing the occlusal line were not taken from subjects with open mandibles and soft tissue measurements were not taken for prosthion and/or infradentale in subjects with folded lips. Table 1 gives a complete list of all landmarks used in this study, their definitions, as well as their corresponding planes and angles of measurement. All soft tissue thickness data collected for chimpanzees has been made available by the authors on Figshare (https://figshare.com/s/8a3ba7df4dad9df7d70d).

Table 1. Cephalometric landmarks including their abbreviations, definitions, planes of measurement, and angles of measurement.

Landmark	Abbreviation	Definition	Plane of measurement	Angle of measurement
Alare	al	Instrumentally determined as the most lateral point on the nasal aperture in a transverse plane	transverse	parallel to reference plane
Bregma	b	Where the sagittal and coronal sutures meet	sagittal	perpendicular to bone
Canine eminence	ce	Most anterior point on the eminence of the maxillary canine	sagittal	perpendicular to bone
Condylion laterale	cdl	Most lateral point on the mandibular condyle	coronal	parallel to reference plane
Ectoconchion anterius	ec(a)	Lateral point of the orbit at a line that bisects the orbit transversely	transverse	parallel to reference plane
Ectoconchion lateralis	ec(l)	Most lateral point of the orbit, at a right angle to ec(a) in the transverse plane	transverse	parallel to reference plane
Ectomolare^2	ecm^2	Most lateral point on the buccal alveolar margin, at the center of the M^2 position	coronal	parallel to reference plane
Ectomolare$_2$	ecm$_2$	Most lateral point on the buccal alveolar margin, at the center of the M$_2$ position	coronal	parallel to reference plane
Euryon	eu	Instrumentally determined as the most lateral point of the cranial vault, on the parietal bone	transverse	parallel to reference plane
Frontotemporale	ft	Most anterior and medial point of the inferior temporal line, on the zygomatic process of the frontal bone	coronal	parallel to reference plane
Glabella	g	Most projecting anterior median point on lower edge of the frontal bone, on the brow ridge, in-between the superciliary arches and above the nasal root	sagittal	parallel to reference plane
Gnathion	gn	Median point halfway between pg and me	sagittal	perpendicular to bone
Gonion	go	Point on the rounded margin of the angle of the mandible, bisecting two lines. One following vertical margin of ramus and one following horizontal margin of corpus of mandible	transverse	parallel to reference plane
Infra canine	iC	Point on the inferior alveolar ridge inferior to the crown of the mandibular canine(s)	transverse	perpendicular to bone
Infradentale	id	Median point at the superior tip of the septum between the mandibular central incisors	sagittal	parallel to reference plane
Infraorbital foramen	if	Most inferior point on the margin of the infraorbital foramen	transverse	perpendicular to bone
Jugale	ju	Vertex of the posterior zygomatic angle, between the vertical edge and horizontal part of the zygomatic arch	transverse	parallel to reference plane
Mentale	ml	Most inferior point on the margin of the mandibular mental foramen	transverse	perpendicular to bone
Menton	me	Most inferior median point of the mental symphysis	sagittal	perpendicular to bone
Metopion	m	Median point, instrumentally determined on the frontal bone as the greatest elevation from a cord between n and b	sagittal	perpendicular to bone
Mid-infraorbital	mio	Point on the anterior aspect of the inferior orbital rim, at a line that vertically bisects the orbit	sagittal	parallel to reference plane
Mid-mandibular body	mmbod	Point on the lateral border of the corpus of the mandible midway between pg and go	coronal	perpendicular to bone
Mid-mandibular border	mmbor	Point on the inferior border of the corpus of the mandible midway between pg and go	coronal	perpendicular to bone
Mid-nasal	mn	Point on internasal suture midway beteen n and rhi	sagittal	perpendicular to bone
Mid-philtrum	mp	Median point midway between ss and pr	sagittal	perpendicular to bone
Mid-ramus	mr	Midpoint along the shortest antero-posterior depth of the ramus, in the masseteric fossa, and usually close to the level of the occlusal plane	coronal	perpendicular to bone

(*Continued*)

Table 1. (Continued)

Landmark	Abbreviation	Definition	Plane of measurement	Angle of measurement
Mid-supraorbital anterius	mso(a)	Point on the anterior aspect of the superior orbital rim, at a line that vertically bisects the orbit	sagittal	parallel to reference plane
Mid-supraorbital superius	mso(s)	Most superior point on the brow ridge, at a right angle to mso(a) in the saggital plane	sagittal	parallel to reference plane
Nasion	n	Intersection of the nasofrontal sutures in the median plane	sagittal	parallel to reference plane
Opisthocranion	op	Most posterior median point on the occipital bone, instrumentally determined as the greatest chord length from g. Note that this points is not necessarily at the tip of the nasal spine.	sagittal	parallel to reference plane
Pogonion	pg	Most anterior median point on the mental eminence of the mandible	sagittal	perpendicular to bone
Porion	po	Most superior point on the upper margin of the external auditory meatus	sagittal	parallel to reference plane
Prosthion	pr	Median point between the central incisors on the anterior most margin of the maxillary alveolar rim	sagittal	parallel to reference plane
Pterion	pt	A circular region, marked by the sphenoparietalis suture at its center. This region marks the thinnest part of the cranial vault.	transverse	parallel to reference plane
Rhinion	rhi	Most rostral (end) point on the internasal suture. It cannot be determined accurately if nasal bones are broken distally.	sagittal	perpendicular to bone
Subnasale	sn	The deepest point seen in the profile view below the anterior nasal spine	sagittal	perpendicular to bone
Supra canine	sC	Point on superior alveolar ridge superior to the crown of the maxillary canine(s)	transverse	perpendicular to bone
Supraglabellare	sg	Deepest part of the supraglabella fossa in the median plane	sagittal	parallel to reference plane
Supramentale	sm	Deepest median point in the groove superior to the mental eminence	sagittal	perpendicular to bone
Vertex	v	Most superior point of the skull	sagittal	parallel to reference plane
Zygion	zy	Instrumentally determined as the most lateral point on the zygomatic arch	coronal	parallel to reference plane
Zygomaxillare	zm	Most inferior point on the zygomaticomaxillary suture	transverse	parallel to reference plane

Landmarks are positioned and measurements taken assuming the FH position.

Points are listed in alphabetical order for ease of reference.

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Intra-observer soft tissue and craniometric measurement reliability was assessed by test-retest measurements following recently discussed data collection protocols in Stephan et al. [32]. Measurements were taken on a subsample of five individuals that were randomly selected by a volunteer. Specimens were PRI-9783, PRI- Akira, PRI-10814, PRI-Mari, and PRI-Reiko. Measurements of each specimen were conducted on separate days over a four-hour period with retest measurements taken seven days after initial assessment for 40 total measuring hours (96 hours including the entire sample). Intra-observer measurement reliability was calculated using the technical error of measurement (TEM) equation:

$$\text{TEM} = \sqrt{\Sigma D^2/2n}$$

Where D is the difference between the values obtained for measurements taken on two separate occasions for each variable raised to the second power and n is the number of individuals measured. The relative TEM (r-TEM) was also calculated by dividing TEM by the mean measurement to convert to a percentage value. The addition of another investigator to determine inter-observer errors was not included in this study as Stephan et al. [32] do not appear to suggest that it is necessary to do both, especially when the entire study is conducted by a single observer.

Two-tail t-tests were used to analyze differences in mean soft tissue thicknesses and craniometric dimensions between males and females as well as between living and deceased subjects. Significance levels were set at $p < 0.05$ but altered according to the Bonferroni adjustment for 39 comparisons of soft tissue thicknesses and 21 comparisons of craniometric dimensions. Post-hoc power analyses were also performed to validate conclusions from two-tail t-tests. These analyses were conducted in Microsoft® Excel®, v. 16.39 for Mac.

Data distribution was checked using the Kolmogorov-Smirnov and Shapiro-Wilk tests. All variables' distributions did not differ significantly from the normal distribution, so no attenuation correction was made. Stepwise multivariate linear regression analysis was then performed to examine the relationships between facial soft tissue thicknesses and craniometric dimensions. Due to the small sample size, missing values in the data set were imputed with variable means rather than using list-wise or pair-wise deletion. These analyses were carried out with the Statistical Package for the Social Sciences (SPSS®) software, v. 26.0 for Mac (SPSS Inc, Chicago, II, USA).

To assess the validity of the regression models, they were tested on an in-group sample of 19 subjects. We admit that it would have been better to perform this test on a separate sample of chimpanzees, rather than the same (training) sample. However, given that the total sample size was already small (n = 19), and no other samples were available, it was decided that it would be better to maintain the largest possible sample size for the regression analyses, rather than removing some individuals to generate a separate out-of-group sample just for validation. With that said, craniometric measurements for each subject, taken from the results of the above described measurement procedure, were employed with the appropriate regression models to predict facial soft tissue thickness at 26 landmarks (8 medial and 18 bilateral). Empirical comparisons were then calculated as the simple difference, z-score and relative percent difference between predicted and observed soft tissue thicknesses. These analyses were conducted in Microsoft® Excel®, v. 16.39 for Mac.

To validate the interspecies compatibility of the regression models, an out-of-group test was conducted on computed tomography scans of one living adult modern human male of European decent and one wet specimen of a deceased sub-adult male bonobo *(Pan paniscus*; subject S9655). Bonobos and chimpanzees are highly similar to each other in many respects, however, they are classified as distinct species [33]. S9655 is a sub-adult (4 years) male and thus outside the age-range of this study sample. Therefore, the bonobo served as an independent test on a sub-adult individual belonging to a separate species that was not used to generate the regression models. Moreover, to the knowledge of the authors, this is the only bonobo scan that is publicly available and as such removes the possibility of selection bias. The bonobo was accessed online via Morphosource (https://www.morphosource.org). The human subject was donated specifically for the purpose of this study to the University of Adelaide by an anonymous donor. Both subjects were obtained as DICOM format bitmap files. Soft tissue measurements used in the comparison between observed and predicted values were taken following the aforementioned protocol and the landmarks are listed in Table 1.

To demonstrate the practical utility of the regression models, a 3D facial approximation was performed on the skull of subjects PRI-Cleo, S9655, as well as on an *Australopithecus africanus* skull (a composite reconstruction of specimens Sts 5 and Sts 52) previously described in Strait et al. [34] and Benazzi et al. [35, 36]. The Sts 5 specimen, dated to 2.14 Ma [37] and found in 1947 at the South African Sterkfontein site by Robert Broom and John Robinson

[38], is a perfect candidate for demonstrating the utility of the facial approximation method. Despite the edentulous maxilla and a break in the cranium associated with a dynamite explosion at the time of discovery, Sts 5 is an exceptionally preserved specimen relative to most other Plio-Pleistocene hominid skulls [39–41]. It is worth nothing here that while the identification of Sts 5 as a female has been and is still the subject of ongoing debate [42–44], the cranial features of the Sts 5 specimen suggest that it was certainly not a subadult individual; therefore, it is well within the age-range of this study sample [45, 46]. The Sts 52 mandible was reconstructed using state-of-the-art digital methods from research quality casts of the original specimen. For a full description of the digital reconstruction process, see S1 Table in Benazzi et al. [35].

To begin the facial approximation procedure, soft tissue thicknesses were estimated for all three subjects by taking craniometric measurements from the skulls in digital format and inserting these measurements into the appropriate regression models. The resulting values were then used to design and place pegs corresponding to the results onto the skulls at their appropriate cephalometric points in Autodesk Maya, 2018 (Autodesk, San Rafael, CA). Both skulls were then 3D printed as recommended by Walker and Humphries [47]. Each skull was printed separately with articulated mandibles on the M200 3D printer (Zortrax®) in acrylonitrile butadiene styrene via fused deposition modelling. Post-processing of prints involved the removal of all support material and then mounting the skulls in the Frankfurt horizontal plane. As a precautionary measure, all three of the 3D printed skulls were measured and cross-checked against measurements taken from their digital counterparts. No discrepancies were observed. The soft tissues were then constructed using an oil-based modelling medium by GV using the pegs to guide the thicknesses at each cephalometric point. Given that facial features (eyes, nose, mouth, and ears) were not the focus of the present study and are likely to be based on intuition rather than empirical science, especially in the case of *A*. *africanus*, the eyes were closed, the nose and mouth were left undefined, and the ears were omitted from all three approximations.

Results

The descriptive statistics for soft tissue measurements and the craniometrics are presented in Tables 2 and 3 respectively, along with the intra-observer TEM and r-TEM for each variable. The mean intra-observer r-TEM for measurements of soft tissue thickness was 2.38%. The lowest intra-observer r-TEM was observed for prosthion (0.45%) and the largest was rhinion (7.00%). For the craniometrics, the mean intra-observer r-TEM was 0.25%. The lowest intra-observer r-TEM was observed for the distance from vertex to subnasale (0.05%) and the largest was for bigonial breadth (0.93%). It may be suggested that the TEM values reported here are underestimates because the repeat measurements were performed on the same scans rather than replicating the whole measurement process to include the reacquisition of scans. However, not only are CT scans of great apes exceptionally rare but also reacquisition of scans of living apes would expose these endangered animals to needless levels of ionizing radiation and is, therefore, unethical.

Two-tail t-tests show that there were no significant differences between living and deceased chimpanzee means across all 39 soft tissue thicknesses (Table 2) and 21 craniometric dimensions (Table 3). This implies that the use of fresh, frozen, and immersed subjects in this study did not compromise the validity of the results. However, post-hoc power analysis revealed that the probability of detecting a significant difference was low and that these results should be taken as tentative. In contrast, post-hoc power analysis revealed that comparisons of sexual dimorphisms were valid. Our results are in agreement with prior research carried out on living

Table 2. Descriptive statistics of facial soft tissue thickness in mm for *Pan troglodytes*.

Variable[a]	Mean	SD	Minimum	Maximum	*n*	TEM[b] (mm)	rTEM[c] (%)
Median points							
v	5.36	2.28	2.40	8.83	13	0.05	0.97
b	4.17	1.50	2.23	7.89	13	0.18	4.55
m	3.29	1.04	1.79	5.44	12	0.19	5.88
sg	3.80	1.56	2.00	8.49	15	0.08	2.18
g	4.00	1.09	2.39	6.13	17	0.20	6.45
n	3.24	0.83	1.98	5.27	19	0.06	1.99
mn	2.33	0.50	1.59	3.42	19	0.06	2.39
rhi	4.07	1.53	1.00	8.31	18	0.26	7.00
sn	7.33	1.94	3.72	12.50	18	0.15	1.70
mp	12.29	4.49	6.42	20.20	12	0.51	3.71
pr	14.06	2.16	10.60	17.85	9	0.07	0.45
id	15.54	3.71	10.10	22.55	14	0.18	0.94
sm	17.79	3.98	10.60	24.35	17	0.43	2.21
pg	12.37	4.18	4.80	19.00	16	0.55	3.35
gn	8.01	3.31	3.17	13.70	17	0.29	2.45
me	5.86	2.04	3.10	10.70	17	0.15	2.35
Bilateral points							
mso(a)	7.25	1.63	4.27	9.73	15	0.11	1.80
mso(s)	4.69	1.39	2.83	7.30	15	0.13	2.34
mio	5.86	2.25	3.01	12.35	19	0.11	1.94
ec(a)	6.01	1.84	1.91	8.81	18	0.21	2.98
ec(l)	7.14	2.91	2.43	12.60	17	0.07	0.81
zy	7.13	2.36	2.54	11.70	18	0.21	2.70
cdl	20.83	5.72	10.33	32.95	18	0.20	0.89
ft	26.97	9.25	13.20	41.73	13	0.53	1.67
pt	34.64	9.10	19.75	56.75	15	0.28	0.77
eu	20.16	7.45	10.21	36.30	12	0.23	1.15
ju	7.99	2.96	3.15	14.60	18	0.16	1.74
if	9.52	1.84	5.70	12.48	19	0.07	0.77
zm	9.17	2.66	2.67	13.23	18	0.09	1.03
ce	11.21	3.74	6.05	18.25	18	0.26	2.27
$\mathbf{ecm^2}$	22.50	6.52	14.93	37.10	19	0.60	2.88
$\mathbf{ecm_2}$	20.04	5.98	12.80	33.50	19	0.60	3.17
sC	9.88	2.19	6.30	13.08	14	0.20	2.02
iC	11.19	2.21	8.41	16.05	18	0.13	1.04
ml	7.17	2.14	3.54	12.25	17	0.31	5.32
mr	26.63	6.70	14.35	44.70	18	0.17	0.59
go	11.44	3.64	5.22	19.78	18	0.51	3.35
mmborder	5.24	2.42	2.15	10.55	17	0.07	1.35
mmbody	13.95	7.15	4.27	34.05	18	0.27	1.58

[a] See variable abbreviations in Table 1.

[b] Technical error of measurement.

[c] Relative technical error of measurement.

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chimpanzees in that there are no significant differences between male and female means [18], with the exception of two soft tissue landmarks (vertex and frontotemporale) and two

Table 3. Descriptive statistics of craniometric dimensions in mm for *Pan troglodytes*.

Variable[a]	Measurement	Mean	SD	Minimum	Maximum	*n*	TEM[b] (mm)	rTEM[c] (%)
v-po	auricular height	65.61	4.14	58.80	73.40	13	0.10	0.15
v-g	distance from vertex to glabella	89.63	6.02	74.60	99.00	12	0.07	0.08
v-n	distance from vertex to nasion	92.45	5.56	78.10	100.00	13	0.11	0.12
v-sn	distance from vertex to subnasale	135.25	7.39	118.30	149.50	13	0.07	0.05
v-gn	distance from vertex to gnathion	198.87	11.98	178.80	228.10	12	0.45	0.23
g-n	supraorbital torus height	11.03	2.51	6.09	15.85	18	0.06	0.56
g-sn	distance from glabella to subnasale	60.84	7.26	36.60	68.20	18	0.13	0.21
g-gn	total face height	140.92	11.63	125.20	167.70	17	0.22	0.16
g-op	maximum head length	142.51	7.29	132.50	153.60	15	0.19	0.13
n-sn	nasal height	53.43	4.55	44.30	61.30	19	0.15	0.29
n-pr	upper face height	86.63	7.91	75.10	101.10	19	0.11	0.13
id-gn	mandibular symphysis height	41.44	5.69	31.00	51.70	19	0.11	0.27
eu-eu	maximum head breadth	97.98	3.90	90.95	104.00	13	0.13	0.13
ft-ft	minimum frontal breadth	45.51	9.21	32.00	66.40	15	0.08	0.18
zy-zy	bizygomatic breadth	131.11	11.05	116.50	156.40	19	0.07	0.05
c-c	intercanine breadth	63.00	7.38	47.60	75.10	19	0.39	0.62
go-go	bigonial breadth	96.39	10.17	79.50	118.50	19	0.90	0.93
al-al	nasal breadth	27.95	1.90	24.40	31.15	19	0.04	0.16
ec-ec	biorbital breadth	91.20	5.26	84.00	102.40	19	0.35	0.39
obh	orbital height	34.54	2.16	29.90	37.50	19	0.08	0.23
obb	orbital breadth	36.13	2.32	31.60	41.38	19	0.08	0.23

[a] See variable abbreviations in Table 1.

[b] Technical error of measurement.

[c] Relative technical error of measurement.

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craniometrics (bizygomatic breadth and inter-canine breadth). The greatest difference between male and female soft tissue measurements was observed for vertex, and the lowest difference for the craniometric was observed for bizygomatic breadth. Note that this means there were only two instances out of 39 soft tissue depths and 21 craniometric dimensions that were significantly different between the sexes.

In stepwise multivariate linear regression analyses, statistically significant ($p < 0.05$) correlations between soft tissue depth measurements (Table 2) and craniometric dimensions (Table 3) were found. Of the 39 cephalometric landmarks assessed, statistically significant regression models were established for 26 landmarks (8 medial and 18 bilateral) and these are given in Table 4. Scatterplots showing four examples of bivariate relationships are shown in Fig 2. As such, it is now possible to reconstruct soft tissue thickness at 44 individual points on the face of chimpanzees using regression models alone. The mean standard error of the estimate (SEE) was 2.39 mm, ranging from 0.42 mm for menton to 5.29 mm for ectomolare$_2$, and the mean multiple correlation coefficients (R = 0.67) far exceed those produced in previous studies of human material [21, 22]. The model with the highest correlation coefficient was pterion (r = 0.93) and the lowest was mid-nasal (r = 0.46). A factor that should be considered here is that if this study sample of chimpanzees was indeed composed of subjects that were scanned in both the supine and prone positions, then the correlations observed here are likely underestimates and the true strengths of correlations higher than those reported.

The results of the regression models applied to the in-group sample of 19 subjects are shown in Table 5. Overall, the performance of the regression models was accurate as the

Table 4. Chimpanzee-derived linear regression models for medial and bilateral facial soft tissue thicknesses.

Variable	Linear regression model[a]	R	SE	*P*
Median points				
Vertex	0.095 (zy-zy)– 0.310 (g-n)– 3.680	0.71	1.40	0.04
Bregma	0.052 (v-gn)– 0.205 (g-n) + 0.048 (g-gn)– 10.689	0.87	0.70	0.04
Metopion	0.113 (v-p)– 0.158 (g-n) + 0.055 (v-sn)– 9.832	0.88	0.42	0.01
Supraglabella	0.149 (v-sn)– 16.370	0.66	1.07	<0.01
Mid-nasal	– 0.040 (id-gn) + 3.996	0.46	0.46	0.05
Subnasale	0.510 (al-al)– 6.942	0.52	1.66	0.02
Prosthion	0.169 (v-g)– 0.064 (g-gn) + 7.897	0.68	1.12	0.02
Menton	0.131 (c-c)– 0.187 (v-n) + 14.818	0.73	1.40	0.02
Bilateral points				
Mid-supraorbital superius	– 0.250 (g-n) + 7.449	0.50	1.09	0.03
Ectoconchion lateralis	0.425 (v-p) + 0.127 (go-go)– 32.987	0.81	1.71	0.01
Zygion	– 0.655 (g-n) + 14.354	0.70	1.70	<0.01
Condylion laterale	1.144 (v-p)– 54.201	0.69	4.11	<0.01
Frontotemporale	0.358 (n-pr) + 0.361 (go-go)– 0.277 (ft-ft)– 0.934 (g-n)– 15.905	0.90	3.72	0.03
Pterion	0.366 (zy-zy) + 0.691 (n-sn) + 0.965 (v-p)– 113.639	0.93	3.26	<0.01
Euryon	0.454 (v-gn)– 70.061	0.73	4.10	<0.01
Jugale	0.573 (v-p)– 29.626	0.67	2.18	<0.01
Infraorbital foramen	0.150 (id-gn) + 3.296	0.47	1.67	0.04
Zygomaxillare	0.416 (v-p)– 18.139	0.54	2.23	0.02
Canine eminence	0.360 (id-gn)– 3.712	0.56	3.09	0.01
Ectomolare^2	0.369 (zy-zy)– 25.860	0.62	5.24	<0.01
Ectomolare$_2$	1.601 (al-al)– 24.708	0.51	5.29	0.03
Infra canine	– 0.110 (v-gn) + 33.154	0.48	1.93	0.04
Mid-ramus	0.523 (go-go)– 23.785	0.82	3.88	<0.01
Gonion	0.628 (v-p)– 29.791	0.60	2.91	0.01
Mid-mandibular border	0.316 (v-p)– 15.491	0.47	2.07	0.04

[a] See variable abbreviations in Table 1.

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differences between observed and predicted soft tissue thickness values were small (mean difference in mm = 1.96 mm; mean z-score = 0.54; mean relative difference 18.13%). The minimum difference in mm was observed in the regression model for *mid-nasal* (0.30 mm) and the maximum for ectomolare ^{2} (5.18 mm) The minimum z-score was observed in the regression model for pterion (0.28) and the maximum for mid-supraobital superius (0.96). The minimum relative difference was observed in the regression model for prosthion (7.62%) and the maximum for mid-mandibular border (28.50%).

Fig 3 shows the results of the regression models applied in 3D facial approximations of subject PRI-Cleo (Fig 3A), the out-of-group bonobo subject S9655 (Fig 3B), and the composite skull of *A*. *africanus* (hereafter referred to as Sts 5; Fig 3C). The differences between observed and predicted soft tissue thicknesses for PRI-Cleo and S9655 were small (Fig 4). The mean difference across 25 landmarks was 1.3 mm for PRI-Cleo (minimum = 0.1 mm; maximum = 5.8 mm) and 1.5mm for S9655 (minimum = 0 mm; maximum = 4.1 mm), which demonstrates that chimpanzee-derived regression models have closely predicted the soft tissue thicknesses for a sub-adult bonobo. In contrast, in the human subject the mean difference across 26 landmarks was 14.5 mm (minimum = 0.1 mm; maximum = 61.5 mm). This difference is much higher than those reported for PRI-Cleo and S9655 and in one case (menton) the regression

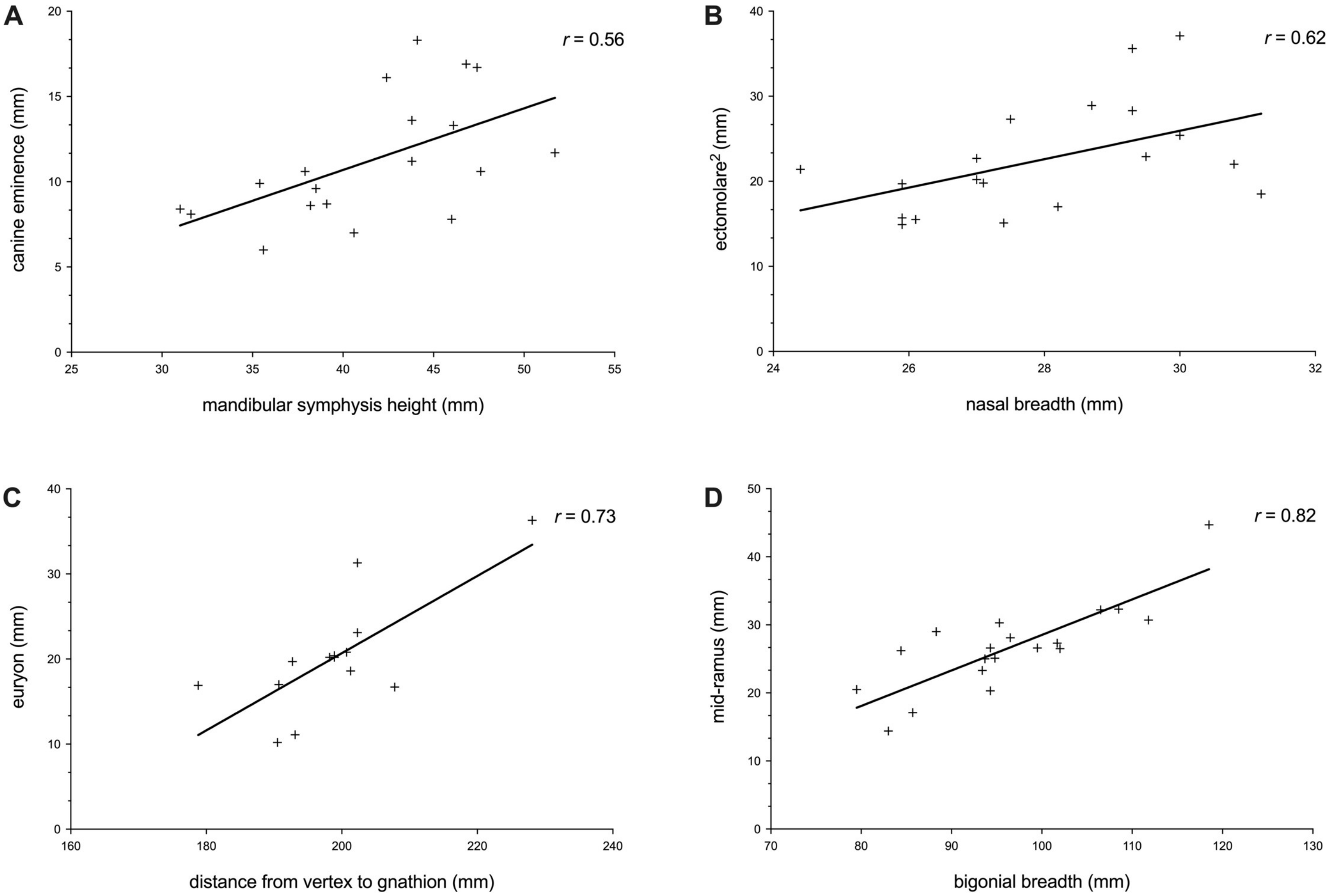

Fig 2. Scatterplots showing four examples of covariation between facial soft tissue and craniometric measurements in chimpanzees. (A) Correlation between canine eminence and mandibular symphysis height. (B) Correlation between ectomolare^2 and nasal breadth. (C) Correlation between euryon and distance from vertex to gnathion. (D) Correlation between mid-ramus and bigonial breadth.

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model produced a negative result, which clearly indicates a fundamental problem with chimp-derived regression models for predicting modern human soft tissue thicknesses. As it is not possible for tissues thicknesses to be negative or equal to zero a 3D facial approximation of the human subject was not produced.

Discussion

Despite the aforementioned limitations of sample size, specimen condition, and complications related to the reacquisition of scans, we have observed that soft tissue thicknesses covary with craniometric dimensions in chimpanzees. Using Stephan's [17] previously published soft tissue thicknesses for humans, a comparison can be made for 23 cephalometric points between *P. troglodytes* and *H. sapiens* means. Fig 5A shows a number of human thicknesses that are more similar to chimpanzees than reported in previous research measuring chimpanzee tissue thicknesses via ultrasound [18]. The thickness of soft tissue in the area of the cheeks, which corresponds to landmarks ectomolare^2 and ectomolare$_2$, has been reported to differ between humans and chimpanzees with humans having thicker cheeks as a result of increased adipose tissue at this region [6, 18]. However, our data show that mean

Table 5. Average differences between predicted soft tissue thicknesses and ground truth values in this study sample of chimpanzees (*Pan troglodytes*).

Variable[a]	Difference (mm)	Z-score	Relative difference (%)	*n*
Median points				
v	1.22	0.51	25.33	11
b	0.57	0.35	15.06	11
m	0.33	0.31	10.59	10
sg	0.96	0.56	24.02	11
mn	0.30	0.61	11.62	11
sn	1.55	0.70	19.18	10
pr	1.14	0.42	7.62	5
me	1.23	0.52	20.13	10
Bilateral points				
mso(s)	1.45	0.96	26.64	11
ec(l)	1.18	0.38	18.35	11
zy	1.44	0.54	21.02	11
cdl	3.32	0.47	16.69	11
ft	2.78	0.30	9.85	10
pt	2.82	0.28	8.77	10
eu	3.79	0.46	21.32	10
ju	1.83	0.56	23.35	11
if	1.42	0.78	14.82	11
zm	2.03	0.63	26.00	10
ce	1.87	0.55	16.55	10
ecm^2	5.18	0.79	22.78	11
ecm_2	3.35	0.62	15.99	11
iC	1.60	0.60	13.90	10
mr	3.33	0.54	14.45	11
go	2.57	0.59	21.64	11
mmbor	1.56	0.61	28.50	10
mmbod	2.27	0.38	17.11	11

[a] See variable abbreviations in Table 1.

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thicknesses at ectomolare$_2$ are identical between humans and chimpanzees and that ectomolare^2 is only marginally larger in humans. Similarly, zygion is identical between species and not smaller in chimpanzees as previously reported. It is worth noting here that since measurements taken by ultrasound are known to compress the tissues of the face in comparison to CT based measurements [32], soft tissue thickness at zygion was most likely underestimated in the previous study [18]. Of the larger differences shown in Fig 5B, there are only slight differences between human and chimpanzee means (minimum = 2 mm; maximum 7.8 mm). It is important to note that this comparison includes only 23 out of the 39 points that were measured in this study and, therefore, a more thorough comparison composed of a larger sample of human values may reveal less similarities than what is reported here. It may be argued also that, based on the similarities identified here, human and chimpanzee means are largely interchangeable and that this may appear like a valid option in the facial approximations of extinct hominids. However, we would like to remind the reader of two problems inherent in using means: 1) means have only been verified for a limited number of landmarks and therefore other regions of the face and head will need to be intuited or the thicknesses interpolated from species specific means; and, more

Fig 3. 3D facial approximations of PRI-Cleo (*Pan troglodytes*; A), 29655 (*Pan paniscus*; B), and composite skull of *Australopithecus africanus* (Sts 5 and Sts 52; C) in right three quarter view (30˚ rotation from full face), norma frontalis and, norma lateralis. Note that the angle of the head in each facial approximation follows standard orientation methods established for modern humans. For *P. troglodytes*, *P.* paniscus, and *A. africanus* this angle may be unjustified biomechanically (Johanson, 1981). Scale bar = 10 cm.

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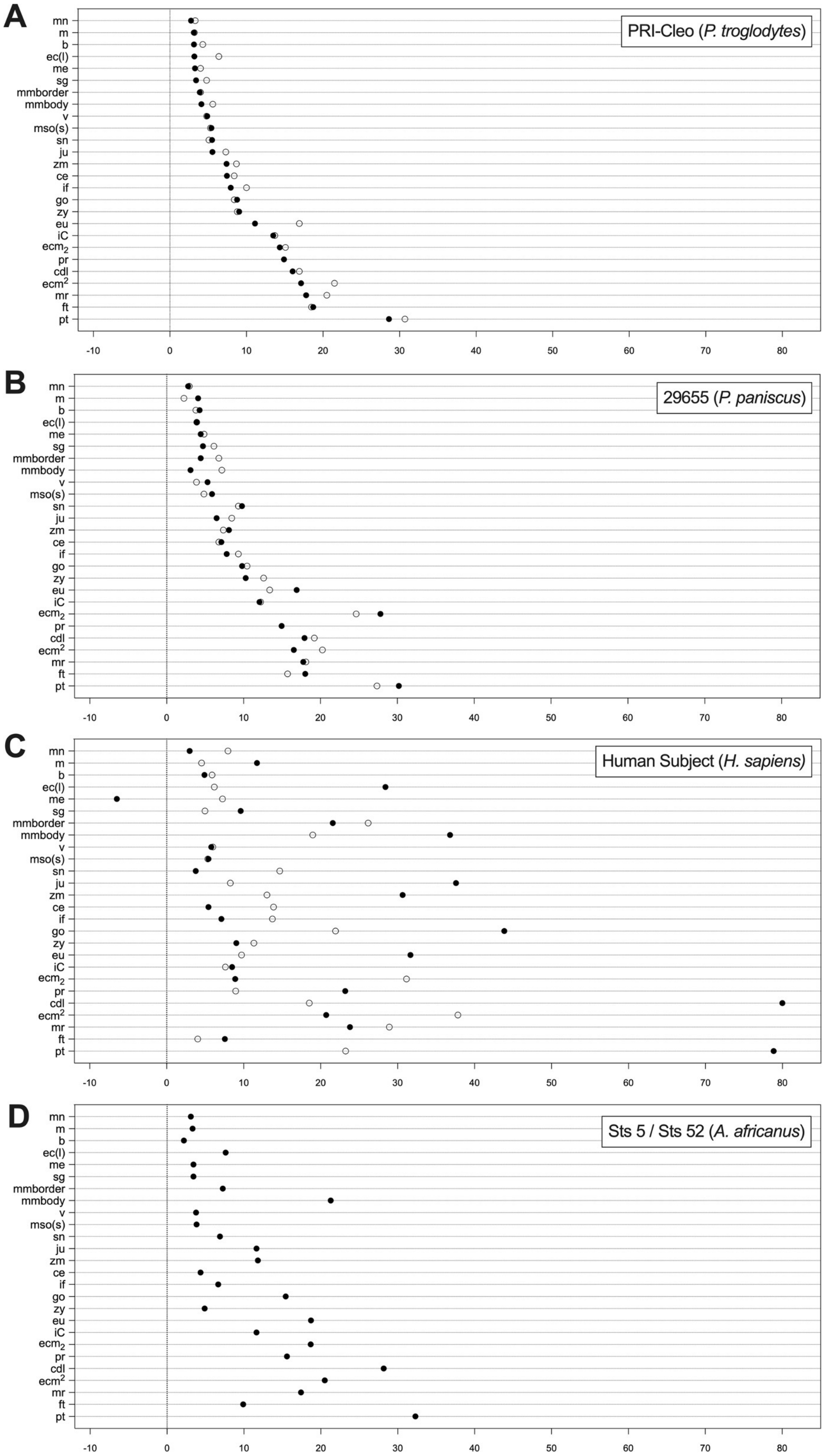

Fig 4. Depth chart comparison of observed (○) and predicted (●) facial soft tissue thickness values between facial approximations of PRI-Cleo (*Pan troglodytes*; A), 29655 (*Pan paniscus*; B), and modern human male of European descent (*Homo sapiens*; C). Predicted thickness values for the composite skull of *Australopithecus africanus* (Sts 5 and Sts 52; D) are also shown. See abbreviations in Table 1.

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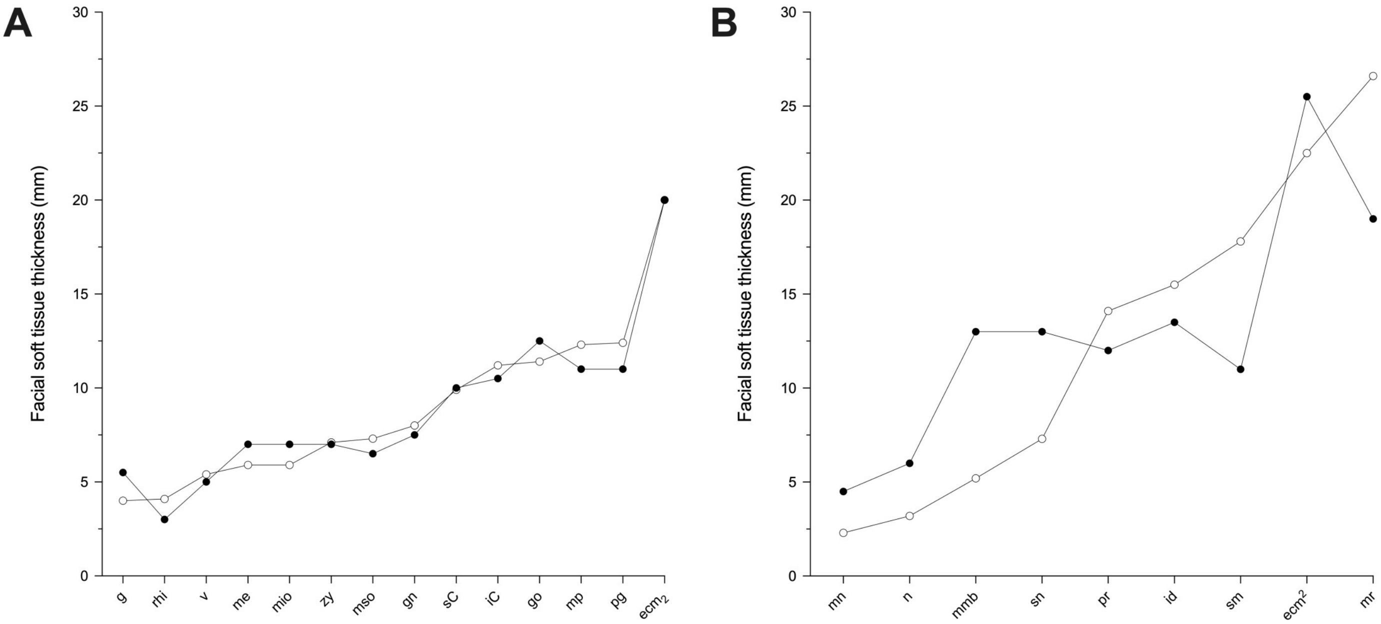

Fig 5. Line charts of *Pan troglodytes* (○) and *Homo sapiens* (●) means comparing values with differences < 2 mm (A) and differences > 2 mm (B).

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importantly 2), means completely ignore variation among individuals. If we had interpolated chimpanzee means into our facial approximation of S9655 the average difference between the observed and predicted soft tissue thicknesses would have been 3.1 mm (minimum = 0.2 mm; maximum = 11.3 mm), which is higher than the average difference of 1.5 mm (minimum = 0 mm; maximum = 4.1 mm) that was produced using the regression models. Furthermore, with regard to our comparison of soft tissue thicknesses and craniometric dimensions between male and female chimpanzees, we have shown that in general they do not display sexual dimorphism and that this does not justify producing separate soft tissue prediction models for males and females because variation between sexes is negligible. In this respect, sexual dimorphism in chimpanzees is similar to modern humans [48], which corresponds with previous analyses of craniofacial sexual dimorphism among extant hominids [49, 50].

The results of the out-of-group tests on the bonobo and human subjects suggest that chimp-derived regression models are compatible with species that have craniometrics that are more similar to chimpanzees than to those of modern humans. As is presented in Table 6 and Fig 6, chimpanzees, bonobos, and modern humans do not equally display disparate craniometric differences. Of the 15 craniometrics taken from S9655, only four were outside the range of variation observed in this study sample of chimpanzees, whereas the human subject presented 11 craniometrics that were outside the range. The slight differences observed in the craniometric dimensions for S9655, however, did not appear to largely affect the predictive accuracy of the regression models, whereas large differences observed in the craniometric dimensions of the human subject produced large estimation errors. With the understanding that the craniofacial morphology of bonobos is similar to chimpanzees, particularly in cranial dimensions and the morphology of the masticatory apparatus, this result is to be expected. We admit that this test was conducted on two individuals only and that this may be perceived as weak evidence for regression model interspecies compatibility, however, we think it unreasonable to assert that all 26 regression models have performed fittingly on the bonobo subject and poorly on the human subject as a result of random chance.

Table 6. Craniometrics taken from skulls of PRI-Cleo (*Pan troglodytes*), 29655 (*Pan paniscus*), composite skull of Australopithecus africanus (*Sts 5 and Sts 52*) and modern human male of European descent (*Homo sapiens*).

Variable^{a}	PRI-Cleo (*P. troglodytes*)	29655 (*P. paniscus*)	Sts5/Sts52a (*A. africanus*)	Human subject (*H. sapiens*)
zy-zy	116.50	**114.90**	125.68	126.40
g-n	8.10	6.22	14.45	8.12
v-gn	178.80	191.55	195.55	**224.30**
g-gn	128.90	130.60	118.25	**116.80**
v-po	61.40	63.05	72.01	**116.80**
v-sn	132.80	141.50	132.90	**174.40**
id-gn	31.00	**30.05**	**22.43**	**25.50**
al-al	24.40	**32.80**	27.10	**21.00**
v-g	90.30	91.20	90.38	**134.70**
c-c	50.60	52.70	**44.50**	**34.00**
v-n	97.20	92.45	92.08	**136.50**
go-go	79.50	79.45	78.80	91.00
n-pr	77.60	86.60	79.85	**67.20**
ft-ft	51.60	**72.05**	**63.98**	**93.50**
n-sn	58.40	59.25	**44.09**	47.80

[a] See variable abbreviations in Table 1.

Bolded text indicates where craniometrics were outside ± two standard deviations from chimpanzee sample means.

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Given that covariation between soft tissue thicknesses and craniometric measurements has been observed in both extant *Homo* and *Pan* species, we hold that it is reasonable to assume that such covariation was present in archaic hominids, such as Sts 5. We submit also that skull morphology is the prime determinant of regression model interspecies compatibility and that chimpanzee-derived regression models are valid for reconstructing the facial appearance of Sts 5. The justification for this is as follows. First, Sts 5's craniometrics were just as different from chimpanzees as S9655's were (Table 6 and Fig 6). We must therefore agree with previous authors [51–53] in that *Pan* appears to be the most suitable extant hominid upon which extrapolations of covariation can be made for *A. africanus*. It is supported by the fact that since the chimpanzee-bonobo split *c.*2 Ma ago there have been no musculoskeletal changes in bonobos [24]. If bonobos had gone extinct *c.*2 Ma ago chimpanzee-derived regression models would still have produced an accurate result. Based on this and the closer affinity of the Sts 5

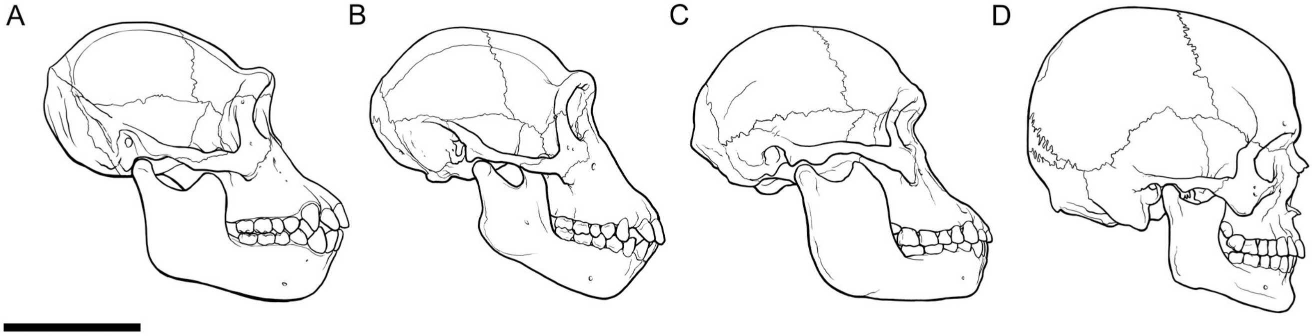

Fig 6. Skulls of PRI-Cleo (*Pan troglodytes*; A), 29655 (*Pan paniscus*; B), the composite skull of *Australopithecus africanus* (Sts 5 and Sts 52; C), and modern human male of European decent (*Homo sapiens*; D) in norma lateralis. Note the similarities and differences in the profiles of the facial projection and their implications for the thicknesses of the muscles that act on the masticatory system between these hominid species. Scale bar = 10 cm.

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skull to *Pan*, any estimation errors in soft tissue thickness for Sts 5 are likely to be similar to or only slightly larger than those of S9655. Second, under the assumption that sexual dimorphism of soft tissue thicknesses in *A*. *africanus* did not differ significantly from chimpanzees and modern humans, it is clear that the lack of consensus surrounding the sex of Sts 5 did not affect the precision of the regression models' predictions. Although we agree with Montagu [54] that the true soft tissue thicknesses for extinct hominids are largely unknowable, we argue that this fact does not diminish the utility of chimpanzee-derived regression models in formulating an informed hypothesis about the facial appearance of Sts 5 and other hominids with similar craniometrics.

To the best of the authors' knowledge, regression models have not been used in the facial approximations of Plio-Pleistocene hominids prior to the present study. Earlier reconstructions have relied heavily on species specific means and/or comparative anatomy of primate muscle morphology [1]. Here we will focus only on the latter as the limitations of means were discussed previously. The location and shape of muscle attachment areas on great ape skulls has been described in detail for bonobos [24], chimpanzees [26], orangutans [55], and gorillas [56], as well as in comparative anatomy textbooks [57]. In any hominid facial approximation, there is an obvious importance in knowing the origin and insertion of the various muscles of the face and head between great apes and humans. However, knowledge of correct anatomical positions of individual muscles is not a substitute for specific estimates for the volumes of the muscles themselves and their coverings, namely the thicknesses of subcutaneous adipose tissues and epithelial linings. Gurche [1] reports being able to systematically determine the size, location, and shape of muscles based on macroscopic surface markings on fossil bones. We will not be surprised if some readers support Gurche's method as found throughout the facial approximation literature is the view that that the face can be reliably approximated from the construction of the facial musculature alone [14, 15, 31]. However, as Ullrich and Stephan [58] have shown, this is a gross misinterpretation of the facial approximation method. In actual fact, facial approximation has always relied heavily on empirical data on soft tissue thicknesses [12, 13, 59]. Gerasimov, for example, implemented soft tissue thickness measurements, only ever placed four muscles onto the skull (the masseter and temporalis muscles), and considered adding any further muscles, such as those of facial expression, to be pointless since their attachments to the skull are not visible. Furthermore, research attempting to recover the size and location of 92 muscles in human material reported that only 23 could be reliably reconstructed from bone alone [60]. Gurche's reconstructions are not necessarily illogical by any means but his approximations are not produced from direct observations of bone as commonly believed [8]. While a practitioner's sculptural skills and anatomical expertise is an obvious benefit in any facial approximation, in isolation the intuited use of this knowledge alone is highly vulnerable to subjective interpretation. For example, soft tissue may be added or subtracted based on personal preference. In contrast, the regression models of the present study provide direct evidence for the approximation of hominid soft tissues. We would like to clarify here that the models do not allow for an entirely speculation-free reconstruction because subjective input is still required to interpolate the surface between landmarks. However, the regression models certainly help to inform any interpolation that is needed. The models may also be useful for studies reconstructing the physiology of extinct hominids. The masticatory system of Australopithecus, for example, may be analyzed in more detail by assigning empirical values to individual muscles of the head. Regression models for mid-ramus, temporal fossa, and euryon reflect the volume of the masseter and temporalis muscles, which may be used to further analyze the biting performance of these hominid species. Regression models may also be extended in future studies to include the postcranial skeleton and improve upon current body mass estimates for extinct hominids [61].

The strong correlations observed in this study certainly raise questions about the claim that soft tissue thicknesses do not covary sufficiently enough with craniometric dimensions to improve soft tissue estimates in craniofacial identification [22]. Given that correlation coefficients generated from regression analysis are sensitive to measurement error and that these errors can only detract from the strengths of association, it is possible that measurement error accounts for some, if not all, of the differences between the correlation coefficients of the present study and those reported in previous studies. The mean intra-observer r-TEMs for soft tissue measurements collected in the present study are lower than the mean intra-observer r-TEM of 8% recorded by Stephan and Sievwright [22], which involved measurements of living human subjects by B-mode ultrasound. The small mean intra-observer r-TEM for the craniometrics in the current study also stands in contrast to the mean intra-observer r-TEM of 2% recorded by Stephan and Sievwright [22]. These results follow the usual trend whereby soft tissue measurements pose a greater challenge to measurement accuracy than the craniometrics. However, they also show that measurements taken from CT scans in OsiriX in the present study are more accurate than measurements taken in previous studies via ultrasound [22]. As stated previously, measurements taken by ultrasound are known to compress the soft tissues in comparison to CT based measurements [32]. It is a basic fact of statistics that random errors reduce covariations and thus produce poorer results of correlations and regressions [62]. Thus, correlations generated from CT based measurements can be expected to be stronger than those obtained from ultrasound measurements. With that said, in the specific case of facial soft tissue thicknesses, it is difficult to evaluate conclusively until further analyses of covariation are made using human material and more reliable CT based measurements.

It is important for us to be transparent about the limitation of the regression models. The aim of any facial approximation is to provide an accurate model of a complete subject. Disappointingly, our regression models offer very little information about the facial features of hominids as they only provide a 3D silhouette upon which facial features can be built. In our approximation of subjects PRI-Cleo and S9655, the facial features can be extrapolated from photographic evidence of great apes as shown in the completed approximations in Fig 7A and 7B respectively. However, for Sts 5 the challenge is further complicated by the fact that practitioners of facial approximation have no direct information to extrapolate the facial features from. Numerous facial approximation studies have developed methods for approximating the facial features in modern humans, although the validity of these methods applied to other hominids has never been tested. Published methods include the approximation of eyeball diameter and anatomical placement in the orbits [63]; eyebrow size, position and shape [64–67]; nasal profile [13, 31, 68–72]; mouth width and shape [12, 14, 31, 58, 73–75]; and size and shape of the external ear [11–13, 67, 76, 77]. Given that facial features are needed to complete any facial approximation, the interspecies compatibility of these methods is worthy of detailed examination in the near future to allow for complete approximations of Plio-Pleistocene hominids to be produced. Until then, the facial features presented in any facial approximation of Sts 5 must obviously remain tentative. For this reason, we chose to present our final reconstruction of Sts 5, shown in Fig 7C, without facial features. While we could have followed in the footsteps of previous practitioners and used our intuition to estimate the facial features, we feel this would only dilute the significance of our results. Mixing up what we know with that which is unknown would only induce confusion. Thus, incomplete as it may be, in Fig 7C we present only what the results of the present study can accomplish. The undefined mass of tissue produced, as a result of the regression models predictions, highlights just how much work there is yet to be done in this domain.

Second, craniofacial morphology among Plio-Pleistocene hominid taxa is highly variable and as such not all fossil craniometrics may fall inside or close to the range modelled in the

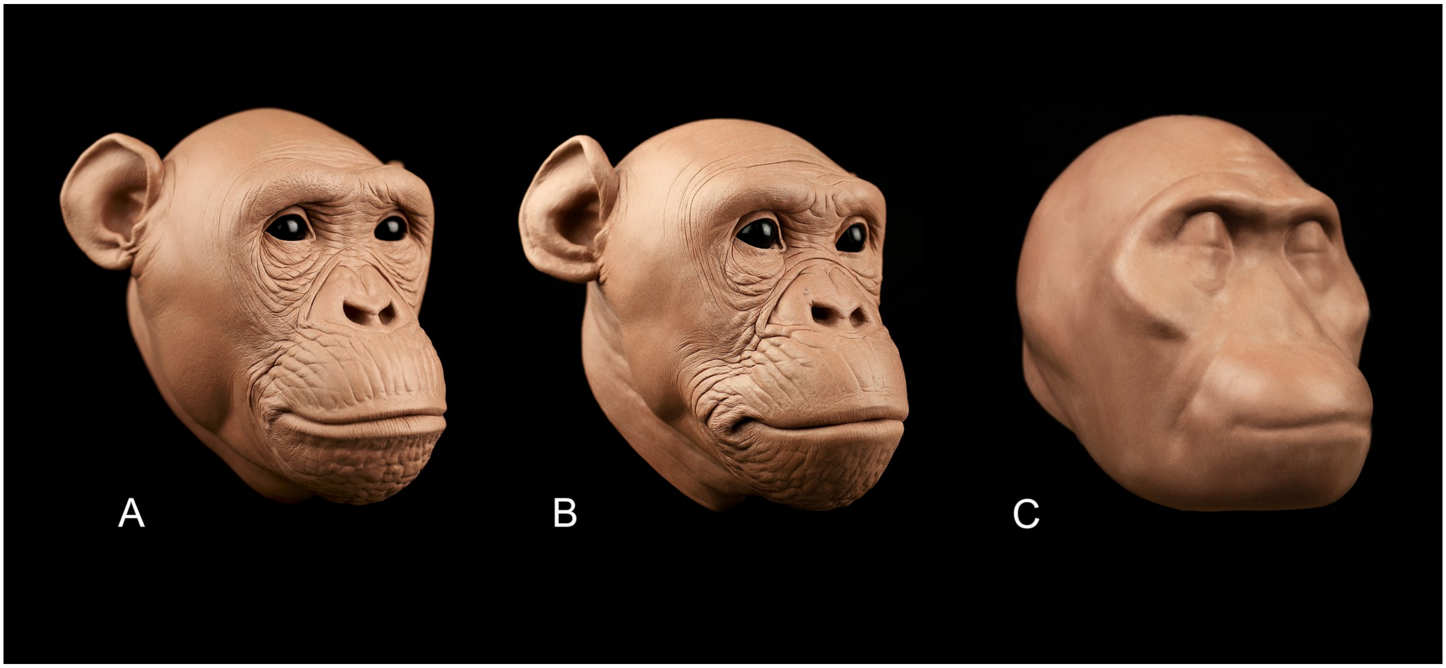

Fig 7. Final facial approximations performed on the skulls of PRI-Cleo (*Pan troglodytes*; A), 29655 (*Pan paniscus*; B), and composite skull of *Australopithecus africanus* (Sts 5 and Sts 52; C). The facial features for PRI-Cleo and 29655 were extrapolated from photographic evidence of chimpanzees and bonobos. The final approximation of *A*. *africanus* represents only what the regression models of the present study can provide. Scale bar = 10 cm.

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present study's regression analysis. Those hominid crania with craniometrics that are at or outside of the extreme ends of the independent variable are likely to produce large estimation errors in soft tissue thickness. As mentioned previously, the craniometrics of Sts 5, as well as subject S9655, are within and close to the range of variation observed in the present study sample of chimpanzees. However, this was not the case for the modern human, which resulted in poor approximation of soft tissue thicknesses, and will not be the case for all hominid skulls, especially specimens with craniofacial morphologies like those exhibited in *Paranthropus boisei* [78, 79]. Repeating stepwise multivariate regression analyses on other extant apes with craniometrics that approximate these fossils, such as gorillas and orangutans, is one possible solution to be explored in future studies.

Finally, it cannot be assumed that correlations observed in adult subjects scale isometrically for very young hominid skulls like that of the Taung fossil or DIK-1 [80, 81]. Changes in modern human soft tissue thicknesses between 0 and 19 years of age have been shown to be small and relatively constant throughout ontogeny [17, 82], but their relations to substantially growing craniometric dimensions may not be the same as in adults. Similarly, thickness changes throughout ontogeny in other primates are unknown, therefore the regression models of the present study may only be viable for approximating adult hominid faces.

Conclusions

The results of this study show that soft tissue and craniometric measurements covary in chimpanzees, which confirms that such covariation is uniformly present in both extant *Homo* and *Pan* species. Chimpanzee-derived regression models appear to be compatible with bonobos but show a marked decrease in predictive accuracy in humans, suggesting that regression model reliability is dependent on craniometric similarity. As the craniometric dimensions of early hominids, such as South African australopithecines, are more similar to chimpanzees than those of humans, chimpanzee-derived regression models may be used to approximate their craniofacial anatomy. Additional relationships between soft tissue thickness and craniometric dimensions of non-human hominids may contribute to more precise facial approximations of early hominids bringing them even closer to standards of objectivity used in forensic sciences. It is hoped that the results of the present study and the reference dataset for facial soft tissue thicknesses of chimpanzees it provides will encourage further research into this topic.

Supporting information

S1 Table. List of specimens used in this study.
(DOCX)

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Investigation: Ryan M. Campbell, Gabriel Vinas, Maciej Henneberg.

Methodology: Ryan M. Campbell, Gabriel Vinas, Maciej Henneberg.

Project administration: Ryan M. Campbell.

Resources: Ryan M. Campbell, Maciej Henneberg.

Software: Ryan M. Campbell, Gabriel Vinas.

Supervision: Ryan M. Campbell, Maciej Henneberg.

Validation: Ryan M. Campbell, Gabriel Vinas, Maciej Henneberg.

Visualization: Ryan M. Campbell, Gabriel Vinas.

Writing – original draft: Ryan M. Campbell, Gabriel Vinas.

Writing – review & editing: Ryan M. Campbell, Gabriel Vinas, Maciej Henneberg.

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Chapter 4: The Nose

Relationships between the hard and soft dimensions of the nose in *Pan troglodytes* and *Homo sapiens* reveal the positions of the nasal tips of Plio-Pleistocene hominids

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Context of Research Article

In the context of forensic facial approximation, the tip of the nose (pronasale) can be regarded as one of the most anatomically meaningful landmarks. Since the nose is in the centre of the face, subjective determination of pronasale position can dramatically alter the nasal appearance, especially for Plio-Pleistocene hominids, whose craniofacial morphology varies from the prognathic, chimp-like Australopithecus to the orthognathic, human-like Neandertals.

In hominid fossils, little is known about the soft tissues of the nose. A common hypothesis for the unique protruding nose of modern humans is that it arose out of the face as an adaptation to climate. However, recent studies have found that the nasal anatomy of modern humans performs poorly at conditioning inhaled air compared with nonhuman primates. Therefore, an alternative explanation for this derived trait is needed to not only improve the accuracy of hominid facial approximations but also to improve our understanding of the craniofacial changes that occurred in the genus Homo.

To develop a method, we took linear and angular measurements from CT scans of 19 chimpanzees and lateral radiographs of 72 modern humans. We performed regression analyses of linear and angular measurements to identify covariation between soft and hard tissues, as well as to examine the length of the nasal cavity in relation to cranial base length and jaw protrusion. To test the compatibility of the method with Plio-Pleistocene hominids, we assessed its interspecies compatibility on a variety of extant non-human primates. These included the bonobo, gorilla, Borneo orangutan, Sumatran orangutan, siamang, and Hamadryas baboon.

Statistically significant correlations were identified in both modern humans and chimpanzees. Slopes and intercepts for both species did not differ significantly. As such, joint prediction formulae could be produced. These formulae were found to accurately approximate pronasale position in all African apes (chimpanzees, bonobos, and gorillas) as well as modern human. Furthermore, the formulae did not appear to be restricted to a given age range as they were found to reliably predict pronasale for sub-adult individuals that were outside of the age-range of the initial chimp-human training sample. Thus, the main contributions of this article are the correlations of pronasale with hard tissues that were found to be homogeneous among humans and African apes and can now be reasonably extended to ancestors leading to the clades, such as Plio-Pleistocene hominids.

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Overall percentage (%): 85%

Certification: This paper reports on original research I conducted during the period of my higher degree by research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.

Signature: ______ ______________________ **Date:** 22 / 02 / 2022

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. The candidate's stated contribution to the publication is accurate (as detailed above);
ii. Permission is granted for the candidate to include the publication in the thesis; and
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RESEARCH ARTICLE

Relationships between the hard and soft dimensions of the nose in *Pan troglodytes* and *Homo sapiens* reveal the positions of the nasal tips of Plio-Pleistocene hominids

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Abstract

By identifying homogeneity in bone and soft tissue covariation patterns in living hominids, it is possible to produce facial approximation methods with interspecies compatibility. These methods may be useful for producing facial approximations of fossil hominids that are more realistic than currently possible. In this study, we conducted an interspecific comparison of the nasomaxillary region in chimpanzees and modern humans with the aim of producing a method for predicting the positions of the nasal tips of Plio-Pleistocene hominids. We addressed this aim by first collecting and performing regression analyses of linear and angular measurements of nasal cavity length and inclination in modern humans (*Homo sapiens*; $n = 72$) and chimpanzees (*Pan troglodytes*; $n = 19$), and then performing a set of out-of-group tests. The first test was performed on four subjects that belonged to the same genus as the training sample, i.e., *Homo* ($n = 2$) and *Pan* ($n = 2$), and the second test, which functioned as an interspecies compatibility test, was performed on *Pan paniscus* ($n = 1$), *Gorilla gorilla* ($n = 3$), *Pongo pygmaeus* ($n = 1$), *Pongo abelli* ($n = 1$), *Symphalangus syndactylus* ($n = 3$), and *Papio hamadryas* ($n = 3$). We identified statistically significant correlations in both humans and chimpanzees with slopes that displayed homogeneity of covariation. Prediction formulae combining these data were found to be compatible with humans and chimpanzees as well as all other African great apes, i.e., bonobos and gorillas. The main conclusion that can be drawn from this study is that our set of regression models for approximating the position of the nasal tip are homogenous among humans and African apes, and can thus be reasonably extended to ancestors leading to these clades.

Introduction

The process of producing faces from dry skulls is known as facial approximation. Since the purpose of this procedure is to estimate the premortem anatomy of individuals as closely as

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possible, each facial feature requires a robust scientific method. While each feature of the face is important in its own right, approximating the position of the nasal tip is critical because the nose is in the center of the face. Approximation error related to nasal anatomy can thus significantly change the facial appearance of the subject in question. For this reason, the tip of the nose (pronasale) is a prominent landmark in the forensic facial approximation literature [1–6].

The pronasale landmark is equally important in facial approximations of extinct Plio-Pleistocene hominids; in this paper hominids means all members of the Hominidae, which is comprised of the African apes, humans, and all ancestors leading to these clades. It has been stated that primate comparative anatomy, which is the study of similarities and differences in structures of different species, is critical to the practice of ancient hominid facial approximation [7]. However, despite numerous facial approximations of extinct hominids presented in scientific textbooks and museum displays, interspecific variation in soft tissue nasal form, or any other feature for that matter, between humans and chimpanzees has received little scientific interest. Although some overlap between human and chimpanzee noses is documented, why modern humans possess a particularly unique projecting, external nose is essentially a mystery. In contrast to human noses, the noses of chimpanzees, and of other great apes (bonobos, gorillas, and orangutans), are relatively flat. Therefore, an investigation into the morphological differences between extant hominids may result in more scientifically robust facial approximation methods, which are needed to reduce the excessive variability recognized in facial approximations of the same individual [8, 9].

For a full overview of the complexities involved in forensic facial approximation, see Stephan et al. [10] and references therein. Here, we discuss only those methods relevant to approximating the nasal profile. In the facial approximation literature, eight methods for approximating the nasal profile in modern humans have been published [1, 3–5, 11–14]. Studies testing these methods [1, 15] have consistently reported that the method by George [12] appears to be the most useful. It consists of calculating a percentage (60.5% for males and 56% for females) of a distance from nasion to the inferior nasal spine to establish a chord at subnasale parallel to the Frankfurt horizontal plane. More recently, Burton et al. [16] found the morphology of the nasal bridge useful for inferring the shape of the nasal tip with very high accuracy and repeatability. Furthermore, orthodontists and maxillofacial surgeons, who also share an interest in nasal morphology, have identified numerous correlations between the soft and hard nasal tissues [17]. These correlations were first explored in Stephan et al. [1], then in Rynn et al. [3], and most recently in Allan et al. [18]. All of these studies have produced regression equations for approximating nasal morphology from dry skulls, although the method by Stephan et al. [1] has been shown to underestimate nasal protrusion [15]. Regardless of the validity and reliability of these methods there are still no serious scientific studies supporting their use on fossil hominids.

Most evolutionary studies of the nasal region have focused on modern humans [19–21] and Neanderthals/Neandertals [22–26]. Conversely, very little attention has been paid to the soft tissue of great ape noses. While we acknowledge that chimpanzee noses have received some research interest [27–29], with the exception of one study [30], gorilla and orangutan studies are practically non-existent. Given that great apes have been useful for understanding the human evolutionary story, it is not clear why the nasal soft tissues of great apes are so understudied. However, it is likely a direct result of the status of these animals as endangered species and the current difficulties involved in obtaining this kind of material (pers. observation).

It has been said that among all the transformations in craniofacial morphology recognized to have occurred during the proposed—although contested (see Kimbel and Villmoare [31])—transition from *Australopithecus* to *Homo*, nasal morphology is a major one [32]. In particular, the nose of modern humans is distinguished from great apes by possessing an external part that protrudes past the piriform aperture. The evolutionary reasons for this feature are the subject of continuing scientific debate. Some studies argue the external nose was derived in the genus *Homo* because of adaptation to climate [33–36]. According to one hypothesis [32], the nose arose out of the face through expansion of the nasal bones relative to the piriform aperture. This is said to have occurred as Pleistocene hominids, such as *Homo erectus*, shifted to increasingly prolonged bouts of physical activity in arid environments, resulting in selective pressures on adaptive respiratory function [32]. In contrast, a more recent study by Nishimaru et al. [37] showed that the external protruding nose in modern humans has little effect on improving air conditioning. They concluded that the unique nasal anatomy in *Homo* was likely formed passively by facial reorganization and not from adaptation to climate. It is important to note that neither of these explanations provide the empirical data needed to approximate the nasal profiles of Plio-Pleistocene hominids. In addition, the question of whether the protrusion growth of the nose was constant or punctuated is entirely unanswered. Obtaining this knowledge is crucial to inform practitioners of facial approximation of how to model the nasal anatomy of their subjects and produce more accurate facial approximations of hominids. Thus, further research is needed to compare the nasal region among extant hominids.

The aims of this study were to explore the matter of Plio-Pleistocene hominid facial approximation further with the focus on predicting the position of the nasal tip. We aimed to (1) compare pronasale position in modern humans and chimpanzees, and (2) to produce prediction formulae for approximating the nasal protrusions of ancient Plio-Pleistocene hominids. We addressed these aims twofold: Firstly, by collecting and performing regression analyses of linear and angular measurements of nasal cavity length and inclination in modern humans (*Homo sapiens*; n = 72) and chimpanzees (*Pan troglodytes*; *n* = 19); and secondly, by performing a set of out-of-group tests consisting of 16 individuals. The first test was performed on four subjects that belonged to the same genus as the training sample, i.e., *Homo* (*n* = 2) and *Pan* (*n* = 2), and the second test, which functioned as an interspecies compatibility test, was performed on *Pan paniscus* (*n* = 1), *Gorilla gorilla* (*n* = 3), *Pongo pygmaeus* (*n* = 1), *Pongo abelli* (*n* = 1), *Symphalangus syndactylus* (*n* = 3), and *Papio hamadryas* (*n* = 3). We hypothesize that soft tissue approximation models, such as those for nasal protrusion, are homogenous among extant hominids and can thus be reasonably extended to all ancestors leading to these clades. To illustrate this hypothesis, we approximated the nasal protrusions for nine fossil hominid specimens. Given the fragile nature of the bones that make up the nasal cavity and how this diminishes the likelihood of their preservation in fossil crania, it was decided to take the least number of measurements needed to produce the prediction formulae. It would simply make no sense, in the context of ancient hominid facial approximation, to produce formulae that require measurements of intricate structures, such as those of the conchae of ethmoid, of extant species if these measurements could not be collected from fossils due to a severely low probability of preservation. Therefore, we only took measurements from aspects of the skull base and maxillofacial skeleton that are most durable and best protected against taphonomic deformation.

Materials & methods

The material used in this study consists of 19 computed tomography (CT) scans of chimpanzee (*P. troglodytes*) heads, previously analyzed in Campbell et al. [38], and 72 lateral cephalometric radiographs of humans. The chimpanzee sample was collected as Digital Imaging and Communications in Medicine (DICOM) format bitmap files from the Digital Morphology Museum, KUPRI (dmm.pri.kyoto-u.ac.jp). The sex ratio for the chimpanzee sample was 1:1.71 (7 male and 12 female) and the mean age 30.9 years (minimum = 9; maximum = 44;

SD = 10.1). A complete list of all the chimpanzee subjects used in this study is presented in the S1 Table. The human sample was collected from the archive of a previous study [39]. The human sample includes two populations from different geographic areas: a Chinese population ($N = 52$), and an American/European population ($N = 20$). The sex ratio for the Chinese sample was 1:0.79 (29 male and 23 female). Exact ages were not available for this group but are classified as young adult. The sex ratio for the American/European sample was 1:0.82 (11 male and 9 female) and the mean age was 19 years and 1 month (minimum = 15; maximum = 32; SD = 4.7). We chose not to investigate sex differences in our samples for the following reasons: First, sex of archaic hominids is often subject to debate in paleoanthropology and, therefore, there is no practical reason to have independent methods for approximating the nasal tip in males and females separately because these methods cannot be confidently assigned to hominids. This is especially the case for those earliest members of the genus *Australopithecus*, such as Sts 5 [40]; and second, the aim of our study is to investigate covariation in soft and hard tissue variables between separate species, not averages of those variables between individuals classified by sex. Ethical approval was not required for the use of human subjects in this study due to the archival and anonymous nature of this material.

Measurements were taken on the midsagittal plane from the chimpanzee DICOM files in OsiriX MD, v. 11.02 (Visage Imaging GmbH, San Diego, USA), and from physical copies of the human radiographs with sliding and spreading calipers. Linear distances were collected using four standard cephalometric landmarks: basion (ba), nasion (n), pronasale (pn), and prosthion (pr) (Fig 1). These four landmarks were positioned onto the skulls and then measurements were taken for cranial base length (ba-n), nasal cavity length (ba-pn), and basion-prosthion length (ba-pr; hereafter referred to as jaw protrusion). All of these measurements were taken according to their descriptions in Martin and Saller [41], which are listed in Table 1. These measurements were chosen because they are relevant to approximating pronasale for the following reasons: 1) cranial base length has been shown to be correlated with other dimensions of the body, such as body height [42] and jaw base size [43]. Cranial base length may therefore be correlated with other dimensions of the body, such as nasal cavity length; and 2) all three of these measurements are generally well represented in the hominid fossil record. As stated in the Introduction, there would simply be no point in taking measurements of intricate structures from extant human and great ape skulls if these measurements could not also be collected from extinct hominid skulls.

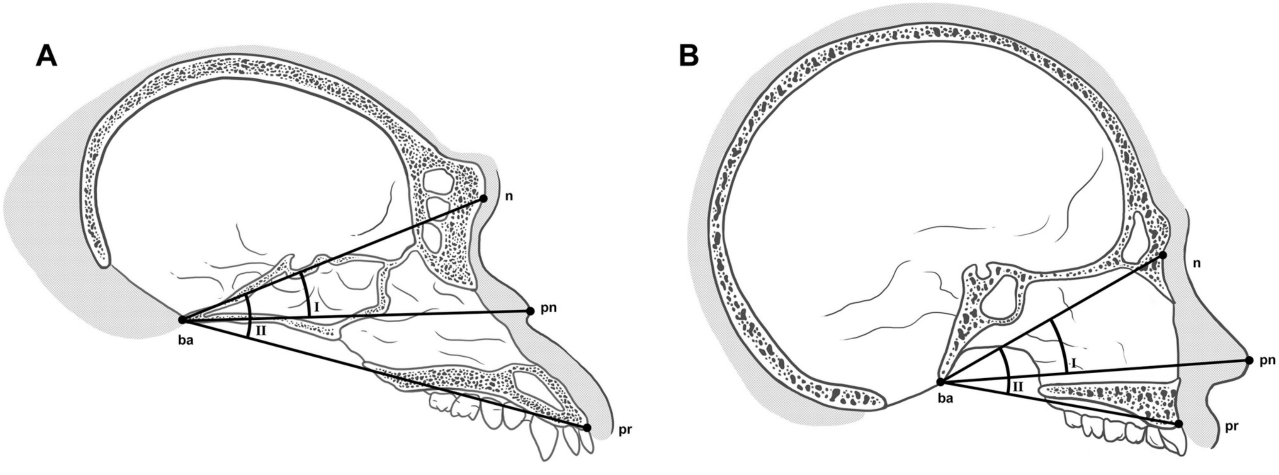

Fig 1. Locations of cephalometric landmarks used in this study and angles measured on the skull of a chimpanzee (*Pan troglodytes*; A) and modern human (*Homo sapiens*; B) in norma lateralis. (I) n-ba-pn angle. (II) n-ba-pr angle. See variable abbreviations in Table 1.

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Table 1. Cephalometric landmarks used in this study including their abbreviations and definitions. Points are listed in alphabetical order for ease of reference.

Landmark	Abbreviation	Definition
Basion	ba	Anteriormost point of the foramen magnum in the midsagittal plane.
Nasion	n	Intersection of the nasofrontal suture in the median plane
Pronasale	pn	The most anterior point of the nose.
Prosthion	pr	The most anterior point of the maxilla in the midsagittal plane.

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Two angles were also measured (na-ba-pn and n-ba-pr) to examine the position of pronasale relative to the hard palate of the maxilla. The vertex of each triangle was positioned at basion with one ray to nasion. This was the starting point for both measurements. The second ray for each angle was positioned at pronasale for the first angle measurement and then to prosthion for the second angle measurement (Fig 1). Measurements were replicated seven days after initial assessment so that technical error of measurement (TEM), and relative TEM (rTEM) could be calculated from test-retest intra-observer measurements. The addition of another investigator to determine inter-observer errors was not included in this study as Stephan et al. [44] do not state that it is necessary to do both. Measurement errors for all variables assessed in this study were less than 0.3% for chimpanzee CT scans and less than 0.9% for human radiographs.

Descriptive statistics were presented for all measurements and their ratios. We then used simple linear regression to examine the relationship of nasal cavity length with cranial base length. We regressed ba-pn against ba-n and assessed intra- and interspecific regression slopes and intercepts using 95% confidence intervals. We further regressed ba-pr against ba-n to compare this relationship with that of the previous for both species, as well as the n-ba-pn angle against the n-ba-pr angle. Reduced major axis (RMA) regression was used to produce the predictive equations because RMA, unlike ordinary least squared regression, is not influenced by random variation of individual measurements around the regression line [45]. All statistical analyses were carried out with the Statistical Package for the Social Sciences (SPSS$^{®}$) software, v. 26.0 for Mac (SPSS Inc, Chicago, II, USA).

To assess the reliability of the RMA prediction formulae, a set of out-of-group tests were performed. In total, the out-of-group test sample consisted of 16 individuals. The first test was performed on four subjects that belonged to the same genus as the training sample (conspecific), i.e., *Homo* (*n* = 2) and *Pan* (*n* = 2), and the second test, which functioned as an interspecies compatibility test (intraspecific), was performed on *Pan paniscus* (*n* = 1), *Gorilla gorilla* (*n* = 3), *Pongo pygmaeus* (*n* = 1), *Pongo abelli* (*n* = 1), *Symphalangus syndactylus* (*n* = 3), and *Papio hamadryas* (*n* = 3). Craniometric measurements were collected from each specimen and used with the appropriate regression model to predict pronasale position. All non-human primate subjects were collected from the Digital Morphology Museum, KUPRI (dmm.pri.kyoto-u.ac.jp), with the exception of the *Pan paniscus* subject (S9655) and the *Pan troglodytes* subject (S12652), which were downloaded from Morphosource (https://www.morphosource.org), as well as the *Pongo abelli* subject. The *Pongo abelli* subject was scanned as part of a health assessment using the Siemens Biograph mCT PET/CT system at the South Australian Health and Medical Research Institute (SAHMRI). Slice thicknesses were set at 0.6mm and the animal was sedated and positioned in the supine position during the scanning procedure. The CT scans were then donated by Zoos South Australia to the University of Adelaide for scientific research. A complete list of all out-of-group test material used in this study and their sources is presented in the S1 Table.

Exact ages for the infant *P. troglodytes* and *G. gorilla* are not provided by KUPRI, so we could only approximate their ages based on the dentition visible in their small immature jaws. In both *G. gorilla* and *P. troglodytes*, eruption of the first permanent molars occurs at approximately three years of age [46]. No permanent dentition eruption is visible in the *G. gorilla* subject, although the first permanent molars, canines, and incisors are approaching eruption. Therefore, PRI-7902 is not much less than 3 years of age. In the *P. troglodytes* subject, only the first permanent molars are fully erupted, so PRI-7895 is similarly approximated as 3 years of age.

In addition to the extant hominids, nasal protrusions were approximated for nine ancient hominid skulls using the RMA prediction formulae. Only hominid fossils with complete crania were selected. The crania included were two specimens representing the *Paranthropus* genus (KNM-WT 17000; *P. aethiopicus* and OH5; *P. boisei*), two specimens representing the *Australopithecus* genus, (Sts 5; *A. africanus* and MH1; *A sediba*), and five specimens representing the genus *Homo* (KNM-ER 1813; *H. habilis*, KNM-WT 15000; *H. ergaster*/*erectus*, LES1; *H. naledi*, Kabwe 1; *H. rhodesiensis*/*heidelbergensis*, and Amud 1; *H. neaderthalensis*/Neandertals). The soft tissue of each hominid was constructed in an oil-based modelling medium by GV using pegs anchored at basion to guide the shape of the nasal profiles and their underlying anatomy. A complete list of all fossil crania in this study and their sources is presented in the S1 Table.

Results

Average cranial base length (ba-n) of chimpanzees was found to be only 3.58 mm (3.3%, z-score = 0.61) greater than that of modern humans (M = 107.86, SD = 5.83, $n = 19$ and M = 104.28, SD = 5.71, $n = 72$ respectively), though T-test results show they formally differ significantly, $p = 0.02$ (2 tail). Average nasal cavity length (ba-pn) of chimpanzees (M = 131.49, SD = 8.03, $n = 19$) is 10.76 mm (8.2%, z-score = 1.34) greater than that of modern humans (M = 120.73, SD = 6.87, $n = 72$), $p < 0.001$ (2 tail). This is approximately two times greater than the difference observed for cranial base length. Average jaw protrusion (ba-pr) of chimpanzees (M = 149.62, SD = 11.20, $n = 19$) is 51.58 mm (34.4%, z-score = 4.60) greater than that of modern humans (M = 98.14, SD = 6.11, $n = 72$), $p < 0.001$ (2 tail). Average n-ba-pr angle of chimpanzees (M = 35.23, SD = 3.46, $n = 19$) is 6.49 degrees (18.4%, z-score = 1.88) smaller than that of modern humans (M = 41.72, SD 2.87, $n = 72$), $p < 0.001$ (2 tail), as is average n-ba-pn angle of chimpanzees (M = 21.60, SD = 2.72, $n = 19$), which is 5.66 degrees (26.2%, z-score = 2.08) smaller than that of modern humans (M = 27.26, SD = 2.27, $n = 72$), $p = 0.02$ (2 tail).

The length of the nasal cavity (ba-pn) was, on average, equivalent to 122.1% and 115.8% of the length of the cranial base (ba-n) in chimpanzees and modern humans respectively, differing by 6.3%. Ratios of nasal cavity length (ba-pn) to jaw protrusion (ba-pr) were diametrically different by 44.4%. The ratio of mean jaw protrusion to cranial base length was 138.7% in chimpanzees and 94.3% in modern humans. In other words, chimpanzees were observed to have a mouth that protrudes past the nasal cavity, whereas modern humans were found to have a nasal cavity that protrudes past the mouth even though lengths of the nasal cavity in both species are relatively similar. These results and descriptive statistics for all measurements are illustrated in Fig 2 and Table 2 respectively.

Simple linear regressions revealed that nasal cavity length (ba-pn) was strongly and significantly correlated with cranial base length (ba-n) in both chimpanzees and modern humans (Table 3). In fact, the correlation coefficients obtained for each species were identical ($r = 0.78$; Table 3). Similarly, n-ba-pn and n-ba-pr angles were strongly correlated in both species with

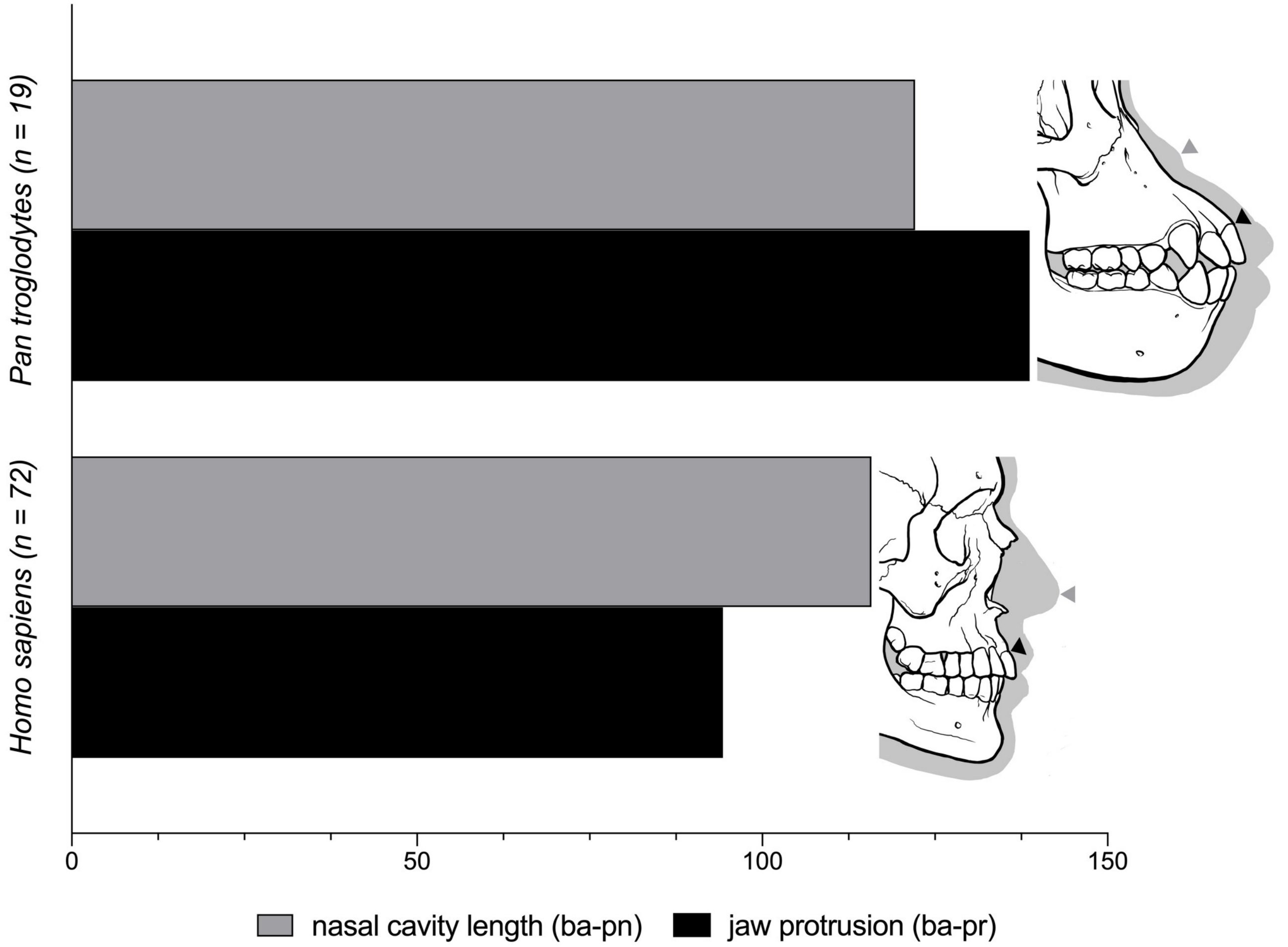

Fig 2. Comparison of nasal cavity length (ba-pn) to jaw protrusion (ba-pr) in chimpanzees (*Pan troglodytes*) and modern humans (*Homo sapiens*). See variable abbreviations in Table 1.

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Table 2. Descriptive statistics for cranial base length (ba-n), nasal cavity length (ba-pn), and jaw protrusion (ba-pr) in mm for chimpanzees (*Pan troglodytes*) and modern humans (*Homo sapiens*). Angles measured in degrees are also shown.

Variable[a]	**Mean**	**SD**	**Minimum**	**Maximum**
Chimpanzee (*n* = 19)				
ba-n	107.86	5.83	98.00	123.00
ba-pn	131.49	8.03	115.90	143.10
ba-pr	149.62	11.20	122.90	163.10
n-ba-pr angle	35.23	3.46	30.26	43.99
n-ba-pn angle	21.60	2.75	16.54	26.92
Human (*n* = 72)				
ba-n	104.14	5.62	92.80	119.20
ba-pn	120.57	7.07	106.30	140.80
ba-pr	98.14	6.11	85.30	114.40
n-ba-pr angle	41.72	2.87	35.50	48.00
n-ba-pn angle	27.26	2.27	21.70	32.00

[a] See variable abbreviations in Table 1.

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Table 3. Ordinary least squares linear regressions of nasal cavity length (ba-pn) against cranial base length (ba-n) and n-ba-pr angle against n-ba-pn angle in chimpanzees and modern humans.

Variable[a]	R	Slope	Intercept	CI[b] Slope Lower	CI[b] Slope Higher	CI[b] Intercept Lower	CI[b] Intercept Higher
Chimpanzee (*n* = 19)							
ba-pn	0.78*	1.07	16.28	0.62	1.51	-31.73	64.29
n-ba-pn	0.83	0.65	-1.39	0.43	0.88	-9.29	6.51
Human (*n* = 72)							
ba-pn	0.78*	0.94	22.89	0.76	1.12	4.12	41.66
n-ba-pn	0.73	0.68	-1.10	0.58	0.78	-5.14	2.93

[a] See variable abbreviations in Table 1.

[b] 95% confidence interval.

* Indicates where correlations coefficients were identical between species.

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chimpanzees ($r = 0.83$) having a slightly greater correlation coefficient than that of modern humans ($r = 0.73$; Table 3). Regression slopes were relatively consistent between species despite the differences mentioned previously regarding nasal cavity length and jaw protrusion. Regressions of nasal cavity length (ba-pn) against cranial base length (ba-n) had a positive slope of 1.07 for chimpanzees and 0.94 for modern humans. Regressions of n-ba-pn angle against n-ba-pr angle had a positive slope of 0.65 for chimpanzees and 0.68 for modern humans. These results show that slopes and intercepts are not species-specific. Subsequent regression analyses combining *Homo* and *Pan* data clearly show this consistency across the entire sample with each combined regression providing a slightly better fit for both species (Fig 3).

Given that simple linear regressions were able to identify statistically significant correlations in the combined sample, as well as establish homogeneity of interspecific covariation, we transformed the prediction equations using Reduced Major Axis (RMA) regressions to remove the influence of individual variation on the predictions. The position of the nasal tip for modern humans and chimpanzees could thus be approximated using the following equations:

$$\text{ba-pn (mm)} = 1.46\,(\text{ba-n}) - 30.32 \pm 5.12$$

$$\text{n-ba-pn (degrees)} = 0.83\,(\text{n-ba-pr}) - 7.42 \pm 1.30$$

The results of the out-of-group tests using the above RMA regression formulae are shown in Table 4. In the conspecific sample (i.e., *Homo sapiens* and *Pan troglodytes*), the average differences between observed and predicted ba-pn length and n-ba-pn angle was 2.3 mm and 0.8 degrees respectively. In the intraspecific sample (i.e., *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*, *Pongo abelli*, *Symphalangus syndactylus*, and *Papio hamadryas*), a substantial difference in the predictive accuracy of the regression models among species was observed (Fig 4). For *P. paniscus* ($n = 1$) and *G. gorilla* (n = 3), the differences were rather small (mean difference for b-pn length = 1.4 mm; mean difference for na-ba-pn angle = 1.2 degrees). For *P. pygmaeus* ($n = 1$), *P. abelii* ($n = 1$), *S. syndactylus* ($n = 3$) and *P. hamadryas* ($n = 3$), the differences were larger (mean difference for b-pn length = 20.8 mm; mean difference for na-ba-pn angle = 2.8 degrees). This clearly indicates that there is an incremental decline in the predictive accuracy of the equations depending on the phylogenetic distance of these species relative to *H. sapiens* and *P. troglodytes*. Interestingly, the accuracy of angle predictions appeared to be affected less by phylogenetic position than length predictions.

It is important to emphasise the ages of several out-of-group test subjects. The ages of the two *Pan troglodytes* subjects was 3 and 5 years, the *P. paniscus* subject 4 years, the infant *G.*

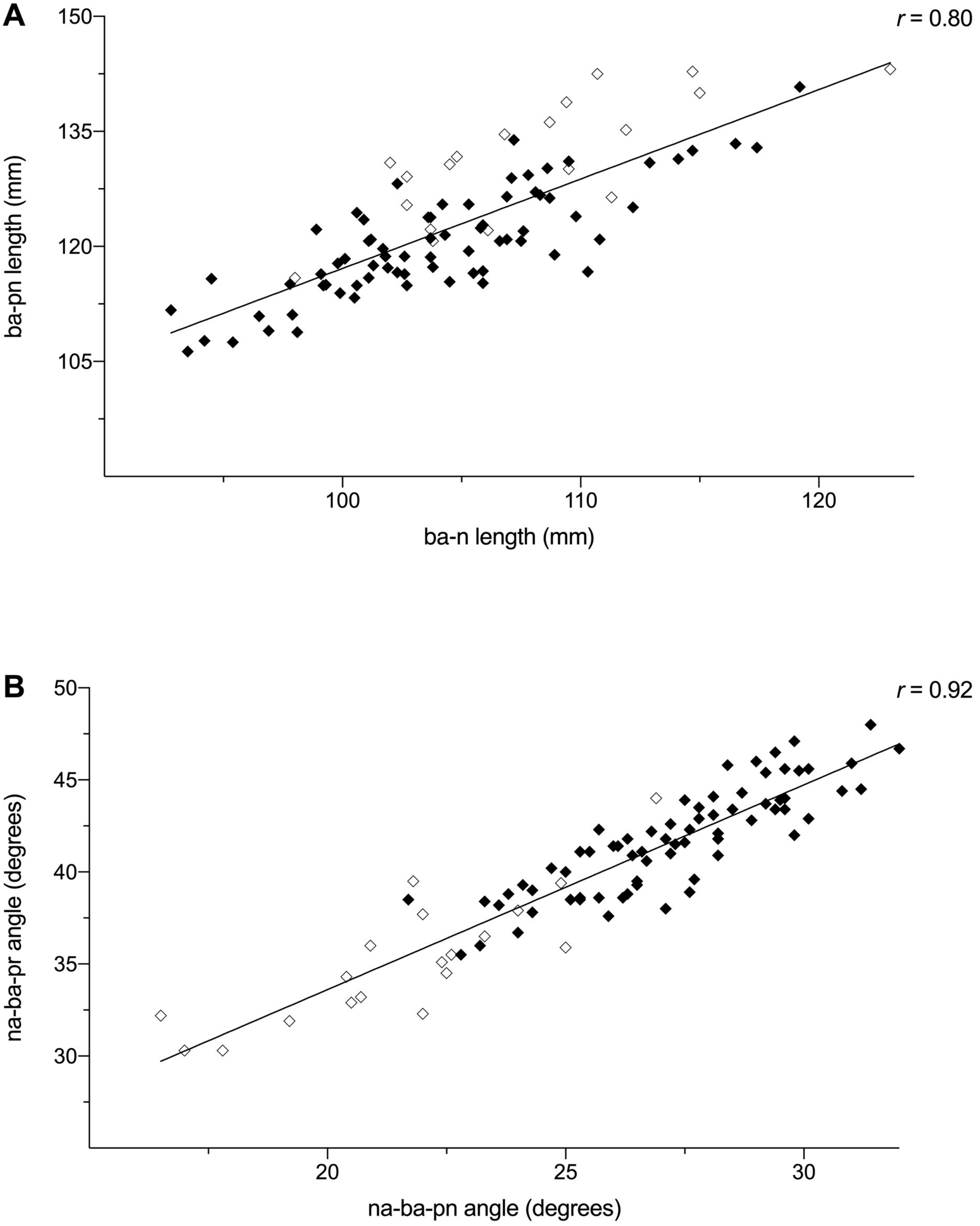

Fig 3. Bivariate scatterplots showing regressions for a combined sample of chimpanzees (*Pan troglodytes*; ◇) and modern humans (*Homo sapiens*; ◆). (A) Regression of nasal cavity length (ba-pn) on cranial base length (ba-n). (B) Regression of n-ba-pr angle on n-ba-pn angle. See variable abbreviations in Table 1.

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Table 4. Average differences between observed and predicted ba-pn length and n-ba-pn angle for subjects used in the out-of-group tests. Subjects listed are grouped by species.

Species	Length difference (mm)	Angle difference (degrees)	Length relative difference (%)	Angle relative difference (%)	*n*
Conspecific sample (*n* = 4)					
H. sapiens	2.1	0.4	1.7	2.3	2
P. troglodytes	2.5	1.2	2.7	4.0	2
Intraspecific sample (*n* = 12)					
P. paniscus	1.1*	0.6*	1.0*	2.0*	1
G. gorilla	1.6	1.8	1.3	6.1	3
P. pygmaeus	10.8*	0.2*	8.7*	1.1*	1
P. abelli	15.4*	1.2*	12.8*	4.5*	1
S. syndactylus	17.4	4.3	21.3	22.4	3
P. hamadryas	39.4	5.5	38.8	16.7	3

* Indicates where values reported are for individuals only.

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gorilla 3 years, the male *G. gorilla* 46 years, and the female *G. gorilla* 54 years. All of these subjects were therefore outside the age-range of the chimpanzee/human training sample. One of the human subjects in the out-of-group test was also outside the age-range of the training sample with an age of 3 years and 9 months. Given that the regression formulae were able to provide quite accurate estimates for all of these subjects (mean difference for b-pn length = 1.6 mm; mean difference for na-ba-pn angle = 1.3 degrees), it appears that when the regression

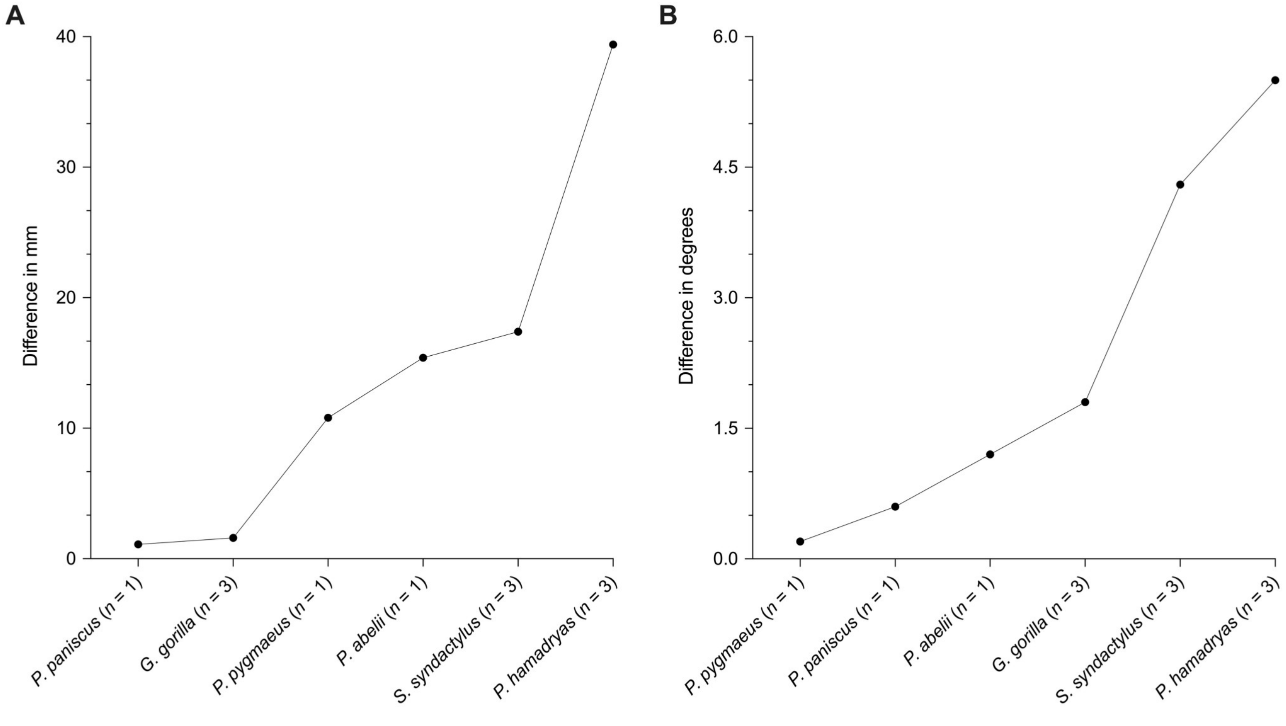

Fig 4. Average difference between observed and predicted values shown for the out-of-group tests performed on six separate species that are outside of the chimpanzee/human training sample. (A) Differences for nasal cavity length (ba-pn). (B) Differences for n-ba-pn angle. Notice the influence of the phylogenetic position of each species relative to modern humans and chimpanzees, i.e., from Hominoidea to Cercopithecoidea, and how this leads to a progressive increase in approximation error.

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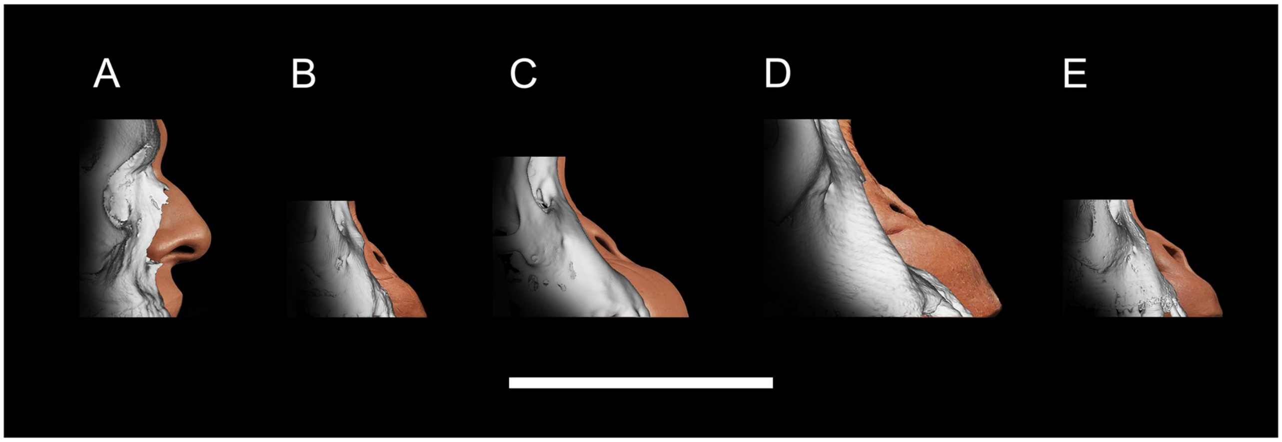

Fig 5. Reduced major axis regression formulae applied in 3D approximations of the nasal region for out-of-group test subjects in norma lateralis. (A) *H. sapiens*: Anonymous 29-year-old male subject. (B) *P. troglodytes*: PRI-7895, 3-years-old. (C) *P. paniscus*: S9655, 4-years-old. (D) *G. gorilla*: PRI-Oki, 54-years-old. (E) *G. gorilla*: PRI-7902, 3-years-old. Scale Bar = 10 cm.

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formulae are compatible with a given species, they do not appear to be restricted to a specific age-range.

The results of the regression formulae applied in 3D approximations of the nasal region for members of *H. sapiens*, *P. troglodytes*, *P. paniscus*, and *G. gorilla* are shown in Fig 5. The formulae of the present study have allowed for the objective and close approximation of the pronasale landmark for all of these species from measurements of their bone alone. 3D approximations were not performed for *P. pygmaeus*, *P. abelii*, *S. syndactylus*, and *P. hamadryas* because, as stated above, the prediction formulae produced poor estimates and are therefore incompatible with these species.

The results of the regression formulae applied in 3D approximations of the nasal regions for extinct hominids are presented in Fig 6. The results are consistent with previous interpretations of these species [7, 47]. There is significant variation in the nasal profile among hominid clades, from the chimp-like profiles of Pliocene *Australopithecus* to the human-like profiles of Pleistocene Neanderthals/Neandertals. Since we have observed that regression formulae derived from modern human and chimpanzee material demonstrate high reliability when applied to all African great apes, i.e., bonobos and gorillas, we put forward the hypothesis that the same formulae are applicable to ancient Plio-Pleistocene hominids and, since the approximations of nasal tip position were not produced using artistic intuition, that our results are empirically and scientifically accurate. The only caveat is that soft tissues of archaic hominids are nonexistent, thus making it impossible to assess the certainty of our results. This matter has been previously discussed in Montagu [48] and continues to burden the practice of Plio-Pleistocene hominid facial approximation today. Therefore, although the formulae allow one to empirically predict the position of pronasale, one must admit that the structures surrounding this landmark offer no certainty in their depictions. Therefore, we present them as informed hypotheses but nothing more.

Discussion

Recently, Campbell et al. [38] showed facial soft tissue thicknesses covary with craniometric dimensions in chimpanzees, and that this allows for predictions of soft tissues from cranial measurements more precisely than by using averages of thicknesses. The present study identified another set of predictable relationships, this time for predicting pronasale position in a

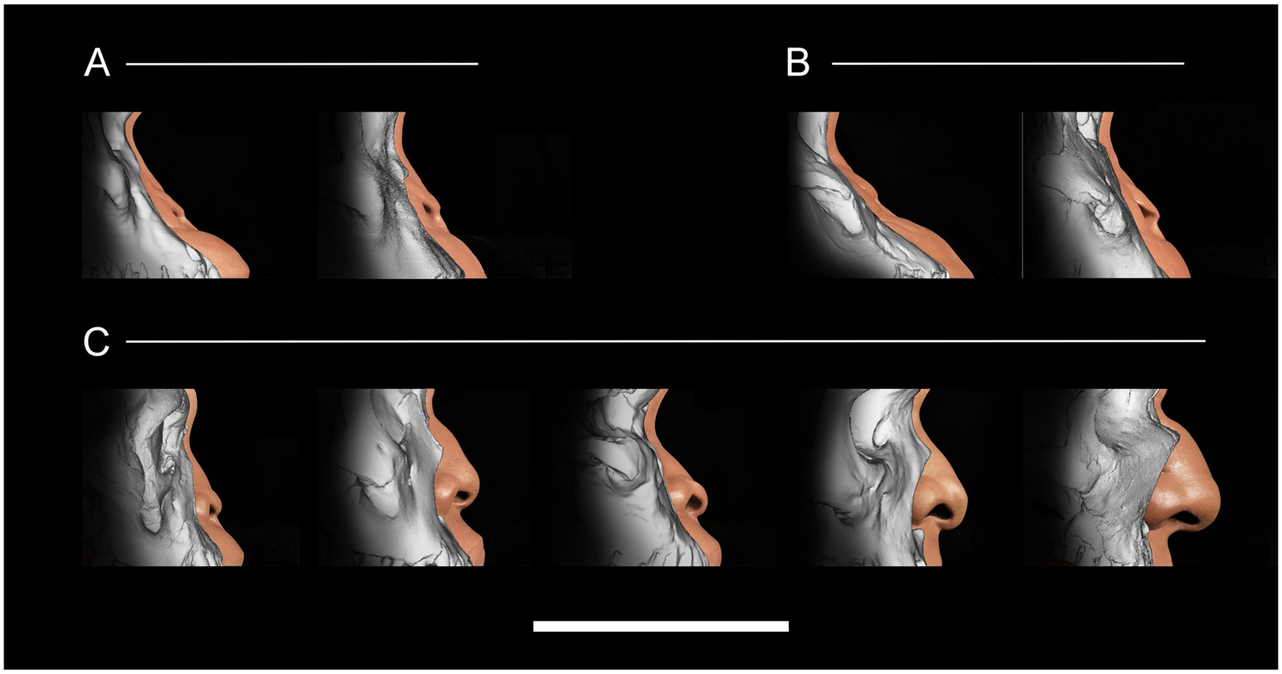

Fig 6. Reduced major axis regression formulae applied in 3D approximations of the nasal region for extinct hominids in norma lateralis. (A) *Australopithecus* genus: Sts 5 (*A. africanus*) and MH1 (*A. sediba*). (B) *Paranthropus* genus: KNM-WT 17000 (*P. aethiopicus*) and OH5 (*P. boisei*). (C) *Homo* genus: KNM-ER 1813 (*H. habilis*), KNM-WT 15000, (*H. ergaster / erectus*), LES1 (*H. naledi*), Kabwe 1 (*H. rhodesiensis/heidelbergensis)*, and Amud 1 (*H. neaderthalensis*/Neandertals). Scale Bar = 10 cm.

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similar way. Studies such as these are revealing that regression models actually outperform averages [18, 38, 49].

The interspecies out-of-group tests show the accuracy of our prediction models worsen with increasing taxonomic difference between humans/chimpanzees and other species. As can be seen in Fig 7, the regression trajectories of *P. paniscus* and *G. gorilla* appear to share a very close affinity with the chimpanzee/human training sample, whereas *P. pygmaeus*, *P. abelli*, *S. syndactylus*, and *P. hamadryas* appear to have group-specific slopes and intercepts that are different from our chimpanzee/human training sample. What is most interesting is that the RMA formulae used to predict pronasale position for the infant and two adult *G. gorilla* subjects produced accurate results, which not only highlights the validity of correlations identified in the present study but also, and more importantly, their compatibility with individuals of different ages belonging to separate species.

Based on the results of the out-of-group interspecies compatibility tests, we suggest that it can be formulated as a general rule that hominids with longer cranial base lengths tend to have longer nasal cavities, and that hominids with maxillae tilted further down from the Frankfurt horizontal plane tend to have axes of the nasal cavity also directed further downwards. Furthermore, since this has been identified in two extant species of hominid, which feature quite distinct skull morphologies, and that the regression models can reliably approximate pronasale position for other African great apes (i.e., *P. paniscus* and *G. gorilla*), these equations can be applied in facial approximation of extinct Plio-Pleistocene hominids. Quantitative linear regression essentially removes descriptive speculation during the approximation of this aspect of the nose for these species.

Owing to the relatively similar measurements of nasal cavity length among the individuals in our chimpanzee and modern human sample, our results are congruent with Nishimura

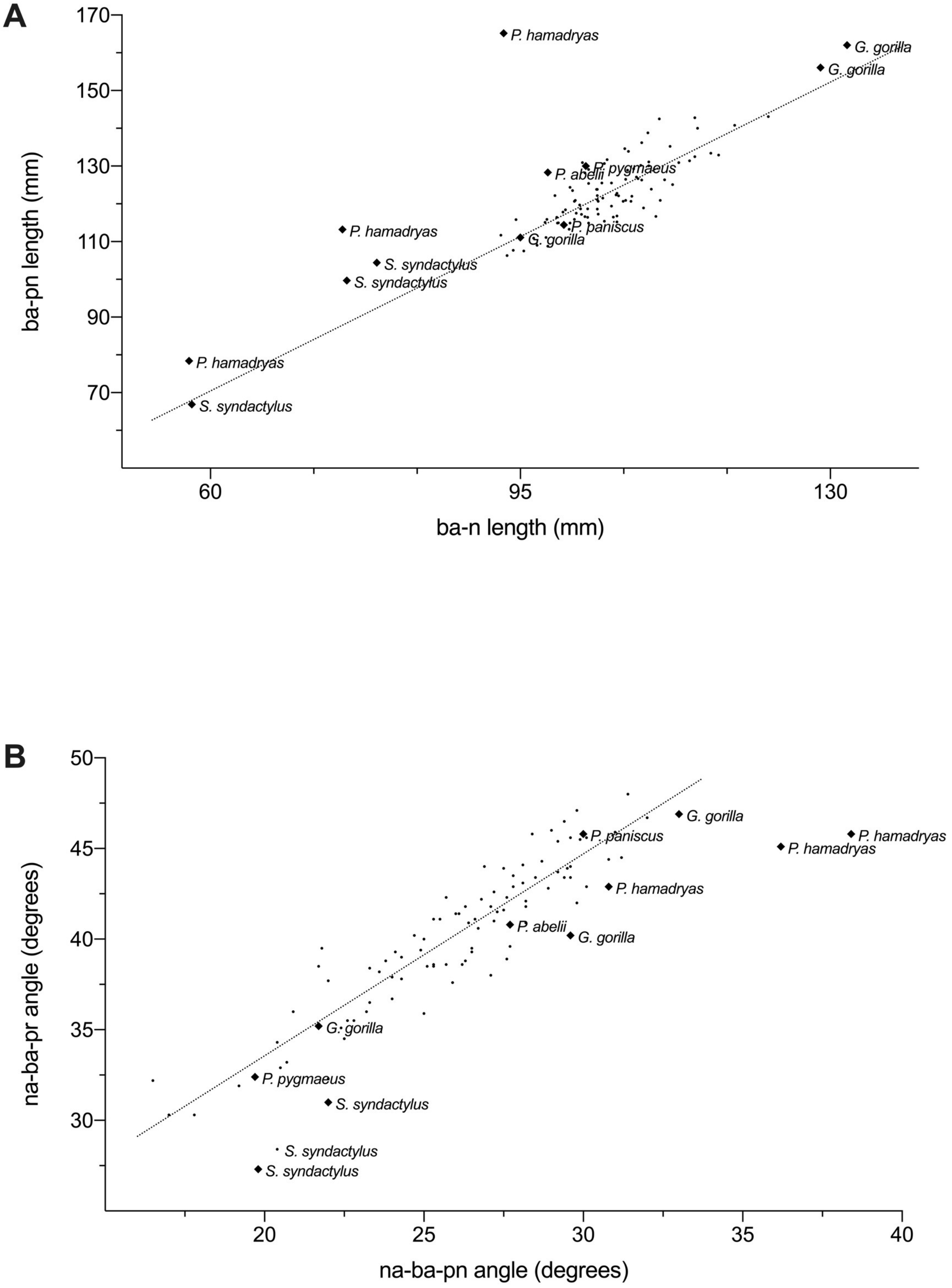

Fig 7. Bivariate scatterplots with actual values for pronasale position in *Pan paniscus* (*n* = 1), *Gorilla gorilla* (*n* = 3), *Pongo pygmaeus* (*n* = 1), *Pongo abelli* (*n* = 1), *Symphalangus syndactylus* (*n* = 3), and *Papio hamadryas* (*n* = 3) superimposed over the chimpanzee/modern human regression lines. (A) Regression of nasal cavity length (ba-pn) on cranial base length (ba-n). (B) Regression of n-ba-pr angle on n-ba-pn angle. See variable abbreviations in Table 1.

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et al. [37] in that projecting noses are only partially a result of local adaptations to climate in the genus *Homo* [32]. Evolving humans entered a variety of habitats from tropical rainforest to open savannah, woodland mosaics, and eventually temperate climate niches [50]. Chimpanzees, on the other hand, did not migrate out of their ancestral environments. Despite this difference, nasal cavity lengths are similar in chimpanzees and modern humans. falsifying the hypothesis that local adaptations to climate included nasal cavity lengths in humans. It seems that nasal cavity length has been retained during human evolution while reductions of the masticatory apparatus reduced face size, thus revealing the prominent nose of modern humans. The nose did not protrude from the face, as previously hypothesized, the face shrunk around the nose exposing it over time. Unlike modern humans, chimpanzees did not evolve the same repertoire of extra-oral methods for predigesting food, nor did they change kinds of foods eaten, and, therefore, did not undergo any reductions in their masticatory apparatus. Furthermore, their social relationships based on male dominance did not allow canine reduction and loss of the C/P3 honing complex [51]. In contrast to changes in food preparation and canine use, neither of the species evolved any extra-nasal methods for conditioning inspired air, which is the most likely explanation for why dimensions of nasal cavity are so strikingly similar between modern humans and chimpanzees. Numerous clinically oriented studies have shown that there are at least two functions of the nose; humidification and temperature modification of inspired air [52, 53]. Nasal cavity length was clearly determined by natural selection for these adaptive roles, whose differences were minimal between great apes and humans relative to changes in the size of the masticatory apparatus.

Our analyses also concur with the observation that modern human facial growth is retarded relative to chimpanzees [54, 55]. This observation has been explored elsewhere in the neotenic theory of the human skull [56], and the self-domestication hypothesis [57]. It suffices to say that during great ape ontogeny, the facial prognathism increases from infancy to adulthood. In contrast, modern human skulls appear paedomorphic relative to chimpanzees. Thus, the developmental changes that occur throughout chimpanzee ontogeny, which result in a mouth that protrudes past the nose, do not occur in modern humans.

Our approximations of Plio-Pleistocene hominids shown in Fig 6 favor the hypothesis that the length of the nasal cavity remained relatively constant throughout human evolution. This point is made obvious by comparing the position of pronasale relative to prosthion between approximations in Fig 6. The more superior position of pronasale and anterior position of prosthion in relation to the piriform aperture, the more chimp-like the nose appears. In direct contrast, the more inferior position of pronasale and posterior position of prosthion, the more human-like the nose appears. Two hominids (KNM-ER 1813; *Homo habilis* and LES1; *Homo naledi*) appear to represent a morphology that is neither ape-like nor human-like. However, the approximations are not outside the realm of possibility of what could have been present in the morphology of intermediate species.

A limitation of this study is the low number of individuals in the chimpanzee sample and out-of-group tests. This is not uncommon for studies of great ape soft tissue due to their sparse availability. It is an unfortunate predicament that researchers find themselves in when studying the soft tissue parts of these endangered and protected animals. Osteological material is plentiful but soft tissue is relatively non-existent. As invaluable as the primate data from KUPRI are, there exists a need for the expansion of publicly available data to include a larger number of living, or recently deceased, individuals. Our solution to this problem is to collect existing data from primate sanctuaries and zoos since a large number of these animals have been scanned over the years for various health reasons (McLelland D. pers. communication). If we can make these data freely available, it would not only benefit researchers but also the public in providing an unprecedented look into the anatomy of our closest living relatives. Such data could also be used to produce anatomically accurate, fully operable surgical training models for veterinarians and comparative anatomists alike. These are planned areas of research.

The other limitation of this study is that it only analyzed the length of the nose, which excludes other elements of the nasal form lateral to the mid-sagittal plane. Although pronasale position is the most defining point for the lateral view of the nose, other features of the nose are arguably as important as the protrusion alone. Alar and nostril size and shape have been somewhat investigated in modern humans but there is still a very wide-open field for researchers to describe these characters in non-human apes. To the knowledge of the authors, Hofer [30] is the only one to have formally studied and published descriptions of the soft tissue parts of the nose in nonhuman apes. In his analysis of gorilla, Hofer [30] recorded many interesting observations regarding their noses, including a number of sulci of the oro-nasal region that are not present in modern humans. The causes for these differences are unclear, so it is worth investigating this material further as explanations for these variations may provide clues to the possible presence of these features in ancient hominids. As such, this points to a large void in the literature requiring that other aspects of the nose receive equal attention in future studies.

Lastly, our modern human sample was composed of members of a USA population derived from Chinese and European backgrounds. It does, therefore, not necessarily reflect the true range of variation across geographically distinct human populations, such as samples of individuals that tend to be more prognathic. However, for the purpose of this study, it is not necessary to include all members of *Homo sapiens*. In the study of regression relationships, details about how prognathism affects the appearance of the nasal tip are provided by the chimpanzee sample. As our data illustrate, although chimpanzees are greatly more prognathic than modern humans, their nasal cavity lengths are relatively similar to those of humans. Therefore, other human populations, such as African populations, are likely to follow the same regression line and have very little, if any, effect on the present studies regression formulae.

Conclusions

There are homogenous relationships between the skull and the soft tissue parts of the nose in both chimpanzees and modern humans as members of the hominid clade. Regressions combining chimpanzee and modern human measurements have shown that this amalgam of data can produce statistically reliable nasal tip location prediction formulae. These prediction formulae can be applied to chimpanzees, modern humans, bonobos, and gorillas. Based on these results, we hypothesize that the same formulae are valid for approximating the position of the nasal tip for extinct hominids because their crania fit into the range of variability present in our sample of extant hominid species. More investigations are needed to produce prediction formulae for other measurements of the soft parts of the nose, such as the ala nasi. Our study does not support the view that the nose arose out of the face. Rather, it provides evidence supporting the alternative hypothesis that reductions in the size of the masticatory apparatus over time led to the external appearance of the anterior part of the nasal cavity in the genus *Homo*.

Supporting information

S1 Table. List of non-human primate subjects included in this study.
(DOCX)

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Validation: Ryan M. Campbell, Maciej Henneberg.

Visualization: Ryan M. Campbell, Gabriel Vinas.

Writing – original draft: Ryan M. Campbell.

Writing – review & editing: Ryan M. Campbell, Gabriel Vinas, Maciej Henneberg.

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Chapter 5: General Discussion & Conclusion

The research undertaken in this thesis has focused on developing a scientific approach to Plio-Pleistocene hominid facial approximation. Because previous depictions of hominids examined by Anderson (2011) displayed considerable variability between approximations of the same specimen, it was inferred that the methods used to produce them were lacking repeatability. The aim of this thesis was to determine if reliable methods could be produced. It was theorised that methods built upon strong empirical foundations would improve approximation accuracy and reduce inconsistencies between depictions of the same individual. The results of this thesis demonstrate that these aims have been achieved through the innovation of an interspecies approach.

5.1 Summaries and chapter reflections

5.1.1 Summary of the review

In Chapter 2, I reviewed and synthesized historical and current literature on forensic facial approximation methods. This was the first time that such a synthesis of knowledge had been constructed with Plio-Pleistocene hominids placed at the forefront of the review. It was necessary to focus on hominids to better understand if there was any scientific basis in applying existing methods to archaic hominid skulls. To accomplish this, I analysed my own facial approximations that I had produced seven years prior to synthesizing this review with two of my colleagues. The important message of this review follows from the clear implication, largely based on the survey by Anderson (2011), that visual depictions of hominids had arisen independent of scientific rigour. This was evidenced by the fact that there was found to be a common failure of practitioner adherence to scientific principles, which had been repeated for decades and led to the accumulation of poorly justified facial approximations. In some instances, scientific methods were borrowed from the forensics literature with little justification for their application to Plio-Pleistocene hominids. Having said this, it is not entirely fair to say that no standards were applied in these approximations, but the standards that were set, which were largely based on intuition alone, were lacking repeatability and the set of specifications needed to enable one to produce an approximation with a high degree of scientific confidence.

5.1.2 Summary of new methods

In Chapters 3 and 4, I produced two new methods that can be used in archaic hominid facial approximation. These methods were produced to address directly, at least in part, the gap in knowledge identified in Chapter 2. The first method that was produced allows for the facial soft tissues of Pliocene Australopithecus to be approximated, which was demonstrated on the *Australopithecus africanus* specimen Sts 5. The second method allows for the approximation of pronasale position for all archaic and modern hominids. The novelty of these methods is their interspecies compatibility. As will be discussed later in this chapter, this is key to understanding why the methods are compatible with archaic hominids, such as *Australopithecus africanus*, and scientifically justified.

5.2 Why this research is an original contribution to new knowledge

This thesis includes three significant original contributions to knowledge: 1) a facial soft tissue thickness dataset for chimpanzees, 2) identification of covariation patterns in non-human primates, and 3) approximation methods with interspecies compatibility.

5.2.1 Facial soft tissue thickness data for chimpanzees

As outlined in Chapter 2, facial soft tissue thickness datasets for adult and sub-adult modern humans have been continuously produced for at least 120 years. Data for non-human primates are non-existent except for one study (Hanebrink, 2006), where facial soft tissue measurements were collected from chimpanzees, although very few measurements were obtained and this was done via B-mode ultrasound, which is not very reliable due to compression of the soft tissues from the measurement device. The larger sample of measurements contained in Chapter 3 improves upon this previous study in three ways: First, by exercising a higher degree of accuracy during measurement collection, mainly due to the measurements being collected from CT scans; second, by adding many measurements that had not been collected before, including new cephalometric landmarks that were invented for chimpanzee heads; and lastly, by reporting the technical error of measurements. In total, 637 soft tissue measurements were manually collected from the faces of 19 chimpanzees, and the resulting dataset can be accessed through an open-access digital data repository.

5.2.2 Covariation patterns in non-human primates

Prior to the work carried out in this thesis, facial soft tissue covariation patterns had only ever been explored in modern humans. Many sceptics still oppose their use, particularly those who have devoted a large amount of time compiling datasets of mean values. Whether covariation patterns were something that existed and could improve facial approximation accuracy is still an open-ended question. However, no one had ever thought to investigate this question by testing to see if covariation patterns could be observed in non-human primates. As stated very early on in the introductory chapter of this thesis, comparative anatomy plays a major role in our understanding of archaic hominids. Plio-Pleistocene hominid facial approximation is no different. In Chapter 3, I clearly show that facial soft tissue thickness at 26 cephalometric landmarks can be reliably approximated for Pliocene Australopithecus using regression formulae derived from observations of covariation in chimpanzees. This is the first time such an observation has been made and should inspire further investigations in samples of modern humans. These investigations will have broader implication for craniofacial identification, as well as facial approximations for archaeid hominis with a closer phylogenetic relationship to modern humans, such as *Homo erectus* and *Homo neanderthalensis*.

5.2.3 Approximation methods with interspecies compatibility

Following on from the discovery that facial soft tissue thicknesses covary with craniometric dimensions in chimpanzees, in Chapter 4 it was shown that not only is their covariation in non-human primates but that at least some of these patterns are homogenous in modern humans and great apes. Regression formulae, therefore, are not always species specific. This supersedes interpolating average facial soft tissue thickness values from one taxon to another, i.e., from Homo to Australopithecus. This would seem to be valid only if facial soft tissue thicknesses were identical between modern humans, great apes, and ancestral hominids which, of course, they are not. Regression formulae produce a solution to this error of interpolation. As was shown in Chapter 3, regression formulae produced from measurements of chimpanzees can be used in approximations of bonobos. Similarly, in Chapter 4, regression formulae for pronasale position can be applied to modern humans, bonobos, chimpanzees, as well as gorillas. Certainly, the covariations seen and shared in modern humans and African apes must be derived from an ancestral state. The only alternative explanation is that the covariations present are a result of parallelism between the extant taxa, i.e., derived and not inherited from a shared ancestor, but this seems unlikely. It seems more likely that the last common ancestors would have had the same covariations now found in modern human and African ape noses. Thus, these covariations can regarded as synapomorphic traits in modern humans, bonobos, chimpanzees, and gorillas.

5.3 Significance to the discipline of biological anthropology

5.3.1 Archaic hominid facial approximation is now a legitimate scientific discipline

In the past, practitioners have worked separately, overly guarding the details of their approximation methods, and never mentioning each other in their written work or formal interviews. This is counterproductive. This thesis contributes to the rise of a new interdisciplinary academic field devoted to archaic hominid facial approximation. This is evidenced in the research conducted in this thesis, as well as other recent scholarly publications concerned with the same subject matter (Campbell et al., 2021a; Campbell et al., 2021b; Hayes et al., 2013; Shui et al., 2021). The significance of this research is a shift from methods that appear to have been based on private observations to methods that have been subjected to empirical tests and have been published. Using open-access publishing of approximation methods allows for the continuation of a collective methodology, rather than one that is kept secret. Secrecy in science only delays progress. Additionally, since there are relatively few tested soft and hard tissue relationships currently known for non-human primates, as well as modem humans, there is huge potential for archaic hominid facial approximation to be an intellectually fruitful field of enquiry that will last for decades.

5.3.2 A strong case for art-science collaboration

This research has shown that scientists and artists can collaborate with no compromise from either side. Artists, like Gabriel Vinas, have ability to produce visually pleasing and technically impressive, like-life approximation of hominids, whereas scientists like myself can systematically construct the methods needed to guide the artist away from interpolating their own biases into their results. Soft tissue measurements at various cephalometric landmarks remove individual interpretation of thickness at those points. Similarly, regression formulae for pronasale position remove individual interpretation of hominid nasal protrusions. Of course, one must admit that neither of these methods provide the means to produce a completely speculation-free facial approximation of a hominid. However, they do provide predictions that constrain artistic freedom for the sake of objectivity. This limitation of freedom may seem repressive for the artist, but I have received recent feedback from an artist embracing these new methods, who states that since they allow for a scientifically stronger approximation, there is no excuse not to use them. Furthermore, giving artists the opportunity to be involved in the construction of new approximation can stimulate discussions on how to improve the efficacy of the methods from an artist's perspective, e.g., adding more cephalometric landmarks on points on the skull beyond the face (Gabriel Vinas, personal communication, December 5, 2021).

5.4 Missteps

5.4.1 Applying existing approximation methods to archaic hominids

At the start of this PhD, there was an early attempt at taking existing approximation methods from the literature, which were based on studies of modern humans, and applying these to Plio-Pleistocene hominids. The first method involved intuitively adding the major muscles of mastication and facial expression over the skull followed by a skin layer (Gurche, 2013). The second method involved predicting soft tissue thicknesses at various landmarks on the face by taking measurements of the skulls and inserting these into equations that were borrowed from Simpson and Henneberg (2002). In the end, these methods were completely incompatible with Australopithecus skulls. However, at the time of preparing this manuscript, I was defending their use. This would turn out to be counterproductive as there were many issues with that manuscript. For example, it included prolonged excurses of a potentially better way to handle facial approximations of Pliocene hominids that unfolded as a stream of consciousness rather than a systematic presentation of results. The manuscript may still be useful for at least exposing the high-handed rhetoric afflicting the practice of hominid approximation, and for exposing the limitations of existing methods, but in hindsight the borrowing of existing methods should not have been defended. More time should have been spent on constructing new ones, such as those described in Chapters 3 and 4.

5.5 What this research does not accomplish

Even though this thesis has achieved a great deal, it must be stated that facial approximation is a complex procedure and there is still a long way to go before one can say that one can produce a facial approximation of any hominid, extant or extinct, that is entirely objective and speculation free. We still do not have an agreed-on standard for approximating Plio-Pleistocene hominid faces, nor the methods required to set this standard.

5.6 Recommendations for future works and extendibility of research methods

5.6.1 Recommendations

Through developing new methods for approximating the facial soft tissue of hominids, this thesis has developed a rigid framework for producing methods with interspecies compatibility, which the author would like to debut here. This framework can act as a springboard for future research developing new methods for those features of the head that were not covered in this thesis. The use of this framework is not straightforward and warrants a detailed explanation here. Figure 5.1. enumerates the phases involved in this framework.

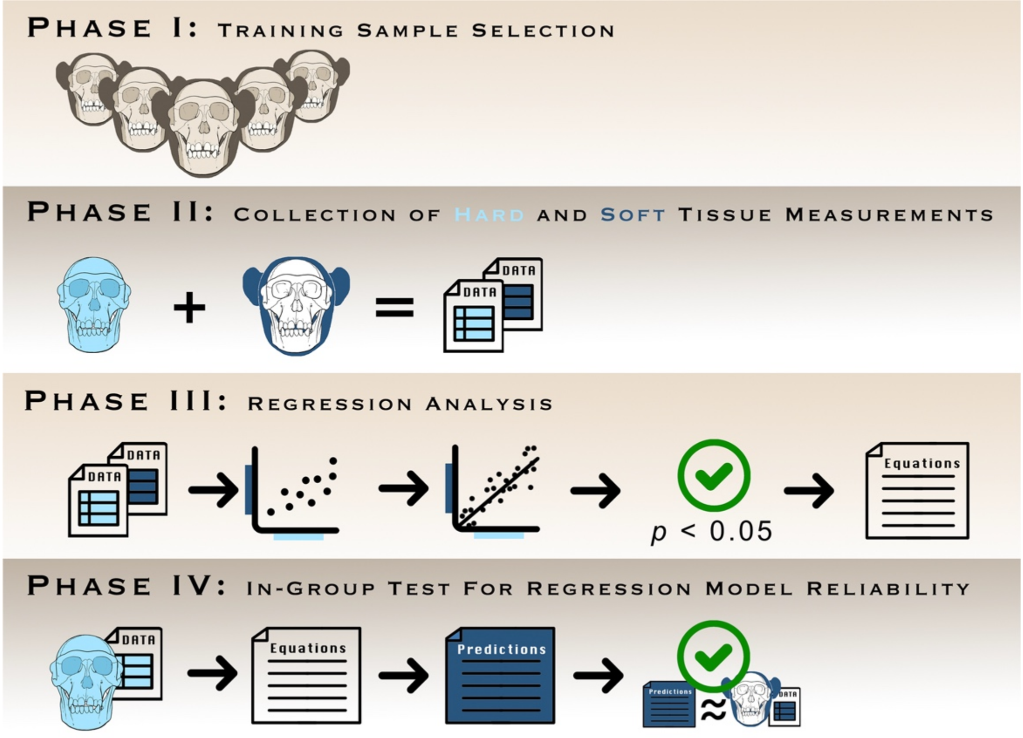

Fig 5.1. Continued on next page

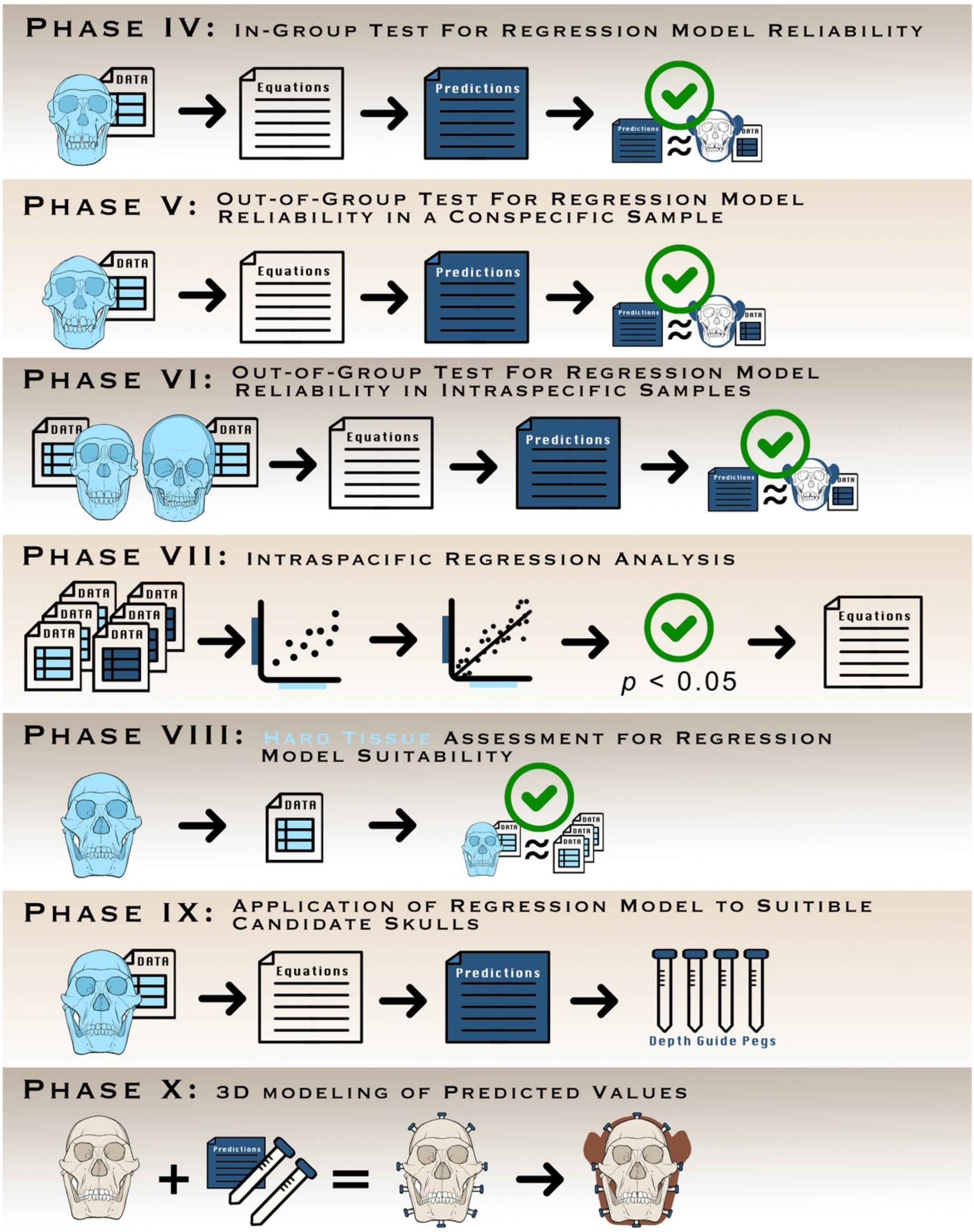

Fig 5.1. Flowchart for constructing soft tissue approximation methods with interspecies compatibility

The framework can be broken down into ten phases. The first phase, phase one, involves selecting a training sample for initial observation. Phase two involves collecting soft tissue and craniometric measurements from various cephalometric landmarks. The author recommends only using the landmarks presented in Chapter 3. Not only is this the most comprehensive set of landmarks ever used in facial approximation including planes of measurement, but it also introduced new landmarks created especially for great apes and are also compatible with Pliocene Australopithecus. It is also advised to not adjust the nomenclature of this set to facilitate comparisons between future studies and allow for easy data pooling. Additionally, intra-observer soft tissue and craniometric measurement reliability should be assessed for each variable using the technical error of measurement equation. If another observer is included in the measurement procedure, then inter-observer technical error of measurement should also be reported. Phase three involves performing regression analyses of the measurements collected in phase two using the soft tissue depths as dependent variables and the craniometrics as independent variables. Depending on how the variables are analysed (bivariate or multivariate), the investigator may explore multiple regression models (i.e., linear regression, polynomial regression, etc.) to find which model provides the best fit. Data distribution should be checked using the Kolmogorov-Smirnov and Shapiro-Wilk tests prior to performing regressions to check for data distribution. It is worth mentioning that some data may be naturally non-normally distributed. For instance, adipose tissue thicknesses tend to be left-skewed. For regression analyses there is a requirement of all data involved in a regression to have the same distribution, i.e., to be homoscedastic. This, however, does not mean all data must be normally distributed.

After correlations between soft tissue and craniometric dimensions have been identified, phase four can commence, which involves testing the resulting regression formulae on the training samples that were used during initial observation. If accurate results are achieved, which can be measured as the simple difference between predicted and actual soft tissue values, the investigator may proceed to phase five. Phase five is a further test of regression formulae reliability. In this phase, the formulae are applied to a sample belonging to the same species as the training sample, but it must be a new sample, i.e., one that was not included in the training sample during phase one's initial observation. Phase six is the first-time separate species are introduced into the framework. The purpose of introducing other species is to test the interspecies compatibility of the regression formulae, as well as identify homogeneity of covariation. If homogeneity of covariation is identified, a final regression analysis is performed, which takes place in phase seven, combining the sample from phase one's initial observation and the separate species introduced in phase six. In phase eight, the investigator may begin to pair formulae with hominid fossils using the craniometrics of the skulls to determine their suitability. Phase nine, involves applying the regression formulae to fossil hominid skulls using phase eight's assessment of suitability to determine the hominid to be approximated. This includes fixings pegs of varying lengths onto the skull at the appropriate cephalometric landmark. The final phase, phase ten, involves modelling the face using the tissue predictions to guide the practitioner's hand. An artist may need to be recruited for this phase as they are specialists in modelling and can provide a sense of realism that takes decades to master.

5.6.2 Extendibility

The above framework could easily be extended to other animals. Assuming that soft tissue covariation patterns are not unique to modern humans and great apes, it is possible that regression formulae may be produced in samples of birds, for example, and used in approximations of similarly sized dinosaurs. The appetite for scientific approximations of these animals was confirmed in a recent paper examining melanin and other pigments in birds for the purpose of interpolating these insights into dinosaurs (Vinther, 2020). The extendibility to extinct vertebrates is only limited by the capability of investigators to obtain soft and hard tissue measurements of extant taxa. As outlined in the framework above, extant samples must be as anatomically close to the extinct species as possible. For example, if one wanted to produce regression formulae for approximating the soft tissue for extinct saber-toothed cats (Machairodontinae), one may take measurements from extant feline. Similarly, if one wanted to produce formulae for extinct Siberian woolly mammoth (*Mammuthus primigenius*) or woolly rhinoceros (*Coelodonta antiquitatisi*), one may take measurements from extant Elephantidine and Rhinocerotine species respectively.

The framework could also be extended to postcranial soft tissues by using regression analyses to produce prediction formulae for hominid bodies. Today, there is only one method currently in the literature for approximating the tissue surrounding hominid bones and it has virtually no empirical basis whatsoever (Gurche, 2013). A more reliable method may be developed by combining general principles of mammal morphology with anthropometric data. For instance, it is known that there is an exponential relationship between body height and body weight (Henneberg et al., 1989). Since cranial capacities of fossil hominids are known (Mathers and Henneberg, 1995), as well as their relationship to body size, these relationships may be useful in approximating general body height and mass. For approximating the mass at specific regions of the body, regressions of lengths of long bones and circumferences of tissues around those bones may exhibit the same covariations observed in chapters 3 and 4 of this thesis.

5.7 Consequences of this research

There is one consequence from the work carried out in this thesis that needs to be accepted. Since we still do not have an agreed-on standard for approximating Plio-Pleistocene hominid faces, new methods must be developed. Consequently, all approximations that are currently presented in museum displays or scientific textbooks for the purpose of education that were not produced using reliable methods must be revised. Until reliable methods are produced for each feature of the face and body, no hominid approximation should be regarded as a definitive depiction. It is the authors belief that one cannot dismiss this statement by simply remarking that facial approximations of Plio-Pleistocene hominids are “artistic interpretations”. If this thesis has shown anything it is that although facial approximations of hominids have been, and still are, produced artistically, they do not always have to be. At the very least, artists should try to ensure that their representations meet the same level of objectivity as the scientific research surrounding their subject matter. Objective methods of soft tissue approximation, the topic of this thesis, do not permit an endless number of possibilities. The fact is that there was only one face to the living Australopithecus who left behind the fossilised skull labelled Sts 5. Scientists and artists need to work together to produce definitive versions of these individuals using scientific principles, not intuition.

5.8 Conclusion

Facial approximation of archaic hominids is a fascinating field. For over 100 years, there has been a clear interest in producing 3D models of these primates, but this work has mostly been carried out by artists. Thanks to an ever-expanding fossil record, new technologies for reconstructing hominid skulls, and the ability to take measurements of modern humans and great apes via computed-tomography, scientist can now collaborate with artists to an unprecedented degree. This thesis demonstrates how beneficial this kind of collaboration can be. While the results of this thesis do not allow for completely speculation-free approximations, they have paved the way for the formulation of new objective methods to produce definitive depictions of Plio-Pleistocene hominids, restoring their appearance for the next generation.

5.9 References

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Appendix

Other Achievements

Industry Engagement

Fusetec, who are a developer of fully operable Medical Training Devices, invited me to their site where I provided my moulding and casting expertise. I was invited to advise on two of their projects to improve their anatomical accuracy using my specialist knowledge of platinum-silicone rubber and polyurethane resin materials.

Creation of an Original Website

Pithecus.org is an online resource dedicated to the study of primate evolution. I created the website with my colleague Gabriel Vinas. It was created as a platform to disseminate new information about human evolution and Plio-Pleistocene hominid facial approximation, which will contribute to student and researcher knowledge at various institutions across the globe. We also donate a percentage of the funds we receive to primate conservation groups, such as the Ape Initiative, Lola la Bonobo, and The Orangutan Project.

The Next Generation of Hominid Reconstructions

Seamlessly blending Art and Science to expand our knowledge of what it means to be human.