Addressing the expanding fossil record by reaching across disciplines

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1 Introduction

The field of paleoanthropology lacks a coherent methodology to approach ontogeny in extinct hominins. In the past two decades, several factors have shifted in paleoanthropology that serve as an impetus to better define this sub-field of study within human evolution. Firstly, the recovery of immature hominin remains has substantially increased and spans multiple genera—*Australopithecus, Paranthropus* and *Homo.* In addition, researchers have begun to recognize the value that sub-adults contribute to the interpretation of an extinct species (e.g., Alemseged et al., 2006; Lordkipanidze et al., 2007; Berger et al., 2010; Bermúdez de Castro et al., 2010; Berger et al., 2015; Martin et al., 2021). Most importantly, paleoanthropologists have associated craniodental and postcranial remains of immature individuals, which means that analysis of maturity patterns are possible on more than one body system in the same individual, for example, brain and dentition, or dentition and skeleton (e.g., Dean et al., 2001; Dean and Smith 2009; Rosas et al., 2017; Cameron et al., 2017; Bolter et al., 2020; Cazenave et al., 2020).

Two of the authors published a 2020 Theory and Synthesis paper *in American Journal of Physical Anthropology* outlining the need to merge the research paradigms of human biology, particularly auxology (growth and development), with evolutionary anthropology research, particularly paleoanthropology and primatology (Bolter and Cameron, 2020). In it, it was argued that paleoanthropology needs a sub-field niche that is developed from existing methods and theory from living ape ontogeny and human auxology studies that can be applied to fossil hominin species (e.g., Zihlman et al., 2004; Smith, 2004; Smith and Boesch, 2011; Jones, 2011; Bromage et al., 2012; Smith et al., 2015; Galbany et al., 2017; Tacail et al., 2019; Gunz et al., 2020; Bolter and Cameron, 2020). Human auxology studies benefit from a robust database, across multiple populations, and with longitudinal studies in order to assess the patterns and variations in typical growth, development and life history stages (e.g., Hauspie et al., 2004; Bogin, 2021). Primate models based on captive and wild longitudinal studies likewise provide a well-developed approach to growth and life history (e.g., Hamada and Udono, 2006; Galbany et al., 2017; van Noordwijk et al, 2018). Synthesizing an approach with shared theory and application to investigate the fossil record will further the understanding of

human evolution and selective pressures shaping maturity patterns in hominin species and provide a collaborative base across research paradigms to integrate data (e.g., Boughner and Rolian, 2016; Antón and Kuzawa, 2017; Jones et al., 2021).

Since the advent of sufficient desktop computer power to run time series analyses, growth modeling to describe the pattern of human growth has become a powerful tool in the Auxologists' armamentarium (e.g., Johnson, 2015). Both parametric and non-parametric models have allowed us to describe not only the pattern of growth but also to investigate the underlying biology of the control of growth and its response to indigenous and exogenous factors (e.g., Eveleth and Tanner, 1990; Wells, 2010; Ulijaszek et al., 2012; Kuzawa et al., 2014; cf. Cameron and Schell, 2021). Thus the intricate interplay of variables acting to create changes in size and shape has been clarified to provide a greater understanding of human growth and potentially non-human ontogeny.

2. *New approaches to studying sub-adult hominins in the fossil record* workshop

Immediately following the 2023 American Association of Biological Anthropology meetings in Reno, Nevada USA, our group met in Minden, Nevada for four days from April 23 – 27 to discuss new approaches to studying sub-adult hominins in the fossil record. Funding for the workshop was provided by the Wenner-Gren Foundation (https://wennergren.org/grantee/debra-r-bolter/).

The goal of the workshop was to provide the opportunity to approach paleoanthropology at the emergence of a sub-discipline of study: sub-adults in the fossil record. The workshop synthesized across three fields—human growth studies, paleoanthropology and primatology—their common language, applications and methods. Researchers from these three fields and across research designs came together to integrate and define a new paradigm for studying immature fossil specimens in human evolution.

16 participants from 5 countries (Australia, Canada, United Kingdom, South Africa and United States) participated in the workshop, ranging from early, mid and late career researchers. (IMAGE 1) 14 participants have published on the topics and 2 participants are early career scientists that served as rapporteurs.

Before the workshop, participants were asked to provide one paper for the group to read that best described the participant's interest or approach to the topic, and two papers that were less specific but of interest that would contribute to the foundation for the workshop discussions. The collated submissions were uploaded to a common web drive the month prior to the workshop (e.g., Appelt et al., 2021; Bernstein, 2010; Bolter

and Cameron, 2020; Berger et al., 2015; Bolter and Zihlman, 2003; Churchill, in press; Cameron, 2015; Hawks et al., 2017; ~~Mahoney et al, 2015~~; Martin et al., 2021; Mahoney et al., 2021; Monson et al., 2022; Pruetz and Bertolani, 2009; Schell and Rousham, 2022; Schroeder, Elton and Ackermann, 2022; Stull, Corron, and Price, 2021; Wolfe and Stull, 2023).

The first evening of the workshop was an informal meet and greet of our participants, as many did not know each other.

The second day began the formal workshop events. Each participant provided a brief biographical introduction. The section leads for human biology (NC), paleoanthropology (SC), and primatology (DB) provided a brief overview of each topic as it related to the study of sub-adults. Breaking research from South African *Homo naledi* was shared as it pertained to the topic of evolution of growth, development and life history (LB). The workshop moderator (JH) summarized the day's discussion and facilitated topics for discussion on day three. During all points of the day there were group discussions to reflect on the ideas presented. That is to say that the workshop format was relaxed, dialogue fluid, and the structure of each day only broadly defined. This format allowed for a conversant flow of thoughts and ideas.

The morning of day three consisted of small group discussions in which participants identified how their science contributed to growth and development research and how this intersected with others in their group. Smaller groups then shared out the main points of discussion, which generated the agenda items for the afternoon discussion and day four agenda. These topics included sample size, vocabulary, health, stressors and somatic indicators of stress, disease, methods to study living and extinct species, adaptation versus random evolutionary forces, variation in environmental conditions and how these affect a species maturity patterns, access to data in paleoanthropology, and public interest in human evolution.

Day four continued the discussion of these topics. The workshop culminated in a summary narrative of 16 main points for future focus in the field of sub-adults in the fossil record:

1. Life stages
2. Energetics
3. Dental and skeletal maturity
4. Brain and body maturity
5. Developmental integration
6. Fossil assemblages
7. Predictions and modeling

8. Shape changes
9. Homo vs heterogeneous fossil assemblages
10. Locomotion effects on maturity
11. Primate data
12. Cross-taxon comparisons
13. Terminology
14. Adaptation and resilience
15. Catalogs (modeling best practices)
16. Public awareness

3 Workshop results and future research

This workshop's main theme was to address the expanding fossil record by reaching across disciplines, generating questions that we can now ask about the fossil record using this multi-disciplinary approach. We concluded that these evolutionary and comparative perspectives should shed light on each species in its own right, rather than limit investigation to what light is shed on modern humans and our evolution. With the increase in fossil populations such as *Homo naledi* comes a new opportunity to investigate pre-adults in an extinct species, in a species morphologically distinct from *Homo sapiens*. One goal of this emerging field is to understand the potential for adaptation and resilience among our living and extinct relatives through investigation of plasticity in maturity patterns.

We identified four main issues moving forward:

1. Identify what is unique in *Homo sapiens* in terms of maturity, growth, development and life history. For example, are humans unique in our long post-infancy and pre-adolescent period? Is the delay in third molar eruption relative to other body systems human-specific? Are prediction points from human models, for example stature, applicable only to humans or do these models hold constant across primates? Apes? Hominins?
2. Define how the study of living populations (humans, non-human primates) provide data and models to apply to fossil population sub-adults. Are maturity events evolutionarily constrained, that is, are co-variations in body systems (e.g., dentition and skeleton; skeleton and menarche) experienced at the individual level, species level or are they phylogenetically broad? Are there developmental integrations of phenotypes common to all primates? Monkeys? Apes? Hominins? Humans?
3. Catalog collections to identify what is available for immature fossil hominin remains. No single database yet exists for hominin fossils. One tangible outcome for the workshop: create a catalog of sub-adult materials

across Africa and Eurasia. Long-term goal: one online meta database of fossil materials.

4. Promote open access to data, not controlled access, and to fossil collections.

The authors are collaborating on a review article for publication.

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IMAGE 1.

From left to right: Front row-Sarah Elton, Tesla Monson, Debra Bolter, Noel Cameron, Julia Boughner. Second row-Patrick Mahoney, Lawrence Schell, Kyra Stull, Keneiloe Molopyane, Robin Bernstein, Jill Pruetz, Third row-Chris Wolfe, John Hawks, Lee Berger, Steve Churchill, Angeline Leece.