# *Homo erectus* as test species for exploring life history variable regression techniques

## K. L. Oleman-Grace

A thesis submitted in partial fulfilment
of the requirements for the degree of
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A thesis submitted in partial fulfilment of the requirements for
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# Declaration

I, Kinsey L. Oleman-Grace, the author, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously been presented for an award at this, or any other, university.

# Abstract

The correlation in Primates of molar emergence age with endocranial volume (ECV), and other life history variables is long established (Smith 1986b, 1989a, 1991a). Regression based predictions of $M_1$Age estimated *H. erectus* $M_1$Age = 4.6—5.0 yr (Smith *et al.* 1995). However, more recent histology calculated $M_1$Age estimates for *H. erectus* indicated an earlier molar emergence for *H. erectus* of 4.0-4.4 yr (Dean *et al.* 2001). The definition of *H. erectus* has evolved as the *H. erectus* hypodigm has increased and now indicates a wider range of ECV for this wide-ranging poly-typical species (e.g. Asfaw et al., 2002; Manzi, 2003; Macchiarelli et al., 2004; Potts et al., 2004; Spoor et al., 2007; Suwa et al., 2007}.

This wider ECV range in *H. erectus* warrants revisiting previous $M_1$Age predictions. Histology derived $M_1$Age estimates of *H. erectus* offer a means of "testing" how accurately $M_1$Age can be predicted. This study asks if regression prediction can be accurate for *H. erectus* $M_1$Age, and whether *H. erectus*-accurate models can also accurately predict other fossil hominin $M_1$Ages. This study revisits these regressions with an updated primate dataset which remains undesirably small and unevenly sampled across the order.

Using a variety of taxonomic groupings and equation types, this study tests 40 regression equation models against four fossil hominin test ranges. While some are accurate for some test points, no model predicts all within accuracy. Residuals for the species used to create the models remain undesirably high. Models cannot accurately predict between species with similar ECV values. Caution is urged in using regression to estimate $M_1$Age in fossil hominins, and regression predicted $M_1$Age should not be used to make inferences about fossil hominin life history patterns in the absence of other life history variable evidence.

# Dedication

GNU Lyn Anderson, who always believed in me. She would have been happy to know that I am wearing bright colours all the time now.

# Acknowledgements

To my supervisors Kevin Kuykendall and Lizzie Craig-Atkins. Thank you for your listening ears, guidance, patience, and support. Thank you to my past advisors: Pia Nystrom and Sue Sherrat for your helpful advice. Many thanks to Inbal Livne and the Powell-Cotton Museum, Quex House and Gardens, Birchington, Kent for granting access to the collection's card catalog, unpublished letters, and field notes. Thank you to William Jungers for answering my query so promptly. Thank you to Amy Chamberlain for her years of thoughtful guidance.

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# Inspirational Quote

"'Aha! The right sort of question!'

'I bet you don't know the answer, though.'

'You are correct. But you must admit it's an interesting question not to know the answer to.'"

Sir Terry Pratchett
*Making Money*, 2007

# Chapter 1

# Chapter 1  Introduction

*Homo erectus* sensu lato was a polytypic hominin species which had an extensive geographic and environmental range. Within the context of the evolution of human life history, *H. erectus* is an interesting species because of its unique suite of similarities and differences with *Homo sapiens*. *H. erectus* was an obligate biped, close in size and shape to anatomically modern humans (hereafter **AMH**), with a dental morphology suggesting a diet similar to that of AMH, but without possessing dental emergence timing that would suggest a fully human-like life history strategy (Wood 1999; Hens *et al.* 2000; Dean *et al.* 2001). *H. sapiens* has life history pattern which is unique both in comparison to other mammals, and more specifically to other primates (Galdikas & Wood 1990; Smith 1991a, b; Hrdy 1992; Leigh & Park 1998; Bogin 1999a, b; Hill & Kaplan 1999; Kaplan *et al.* 2000; Key 2000; Worthman 2003; Bogin 2009; Atsalis *et al.* 2010; Kuzawa & Bragg 2012). Historically, paleoanthropology focused on reconstructing fossil hominin life history as a means to exploring the pace and pattern of the evolution of *H. sapiens* life history pattern (Smith 1989b; Skinner & Wood 2006; Robson & Wood 2008; Smith *et al.* 2010b). *H. erectus* is the earliest species whose placement within the genus *Homo* is not under debate (Wood 1999). Consequently, the reconstruction of *H. erectus* s.l. life history patterns has been of particular interest, historically, within paleoanthropology.

One method for predicting fossil hominin life histories is to use regressions of extant primate timing of the emergence of the lower first permanent molar (hereafter $M_1$Age) and endocranial volume (hereafter ECV)[1] data (Smith 1986a; Smith *et al.* 1995). Historically, these regression equations were applied mean ECV for *H. erectus* s.l. and some Australopith[2] fossil specimens to predict the $M_1$Age of those species (Smith *et al.* 1995). The Australopiths were predicted as 'ape-like', *H. habilis* as intermediate, *H. erectus* $M_1$Age at 4.75±0.25 yr, which fell within the AMH range. Applying human or chimpanzee regressions returned $M_1$Ages for *H. erectus* from 4.4±0.2 to 5.15±0.25, respectively. Like dental regressions, other types of life history related variable regressions (such as neonatal ECV to adult ECV) have been applied not only to predict an "ape-like" life history pattern (and a very late evolution of human-like life history traits in our evolutions) in *H. erectus* but also the absence of language or other higher level cognition in the species. Not long after the publication of this $M_1$Age prediction study, one of it's authors highlighted where regression predictions can be misapplied: in this case the highly correlated ($r = 0.97$) body mass by first mandibular molar area relationship (Smith 1996). Body mass for the extant species used in the equation was predicted with error percentages up to ±121%. Smith highlighted that the estimates of fossil species traits presented in many quantitative studies were presented as precise values which could be "expressed with more apparent certainty than the equation can predict for the extant species used to create the equation" (1996:460).

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[1] this can also be referred to as 'brain size', 'cranial capacity', or 'endocranial capacity' in the literature

[2] Australopiths used to refer to *Australopithecus* and *Paranthropus* throughout unless otherwise specified

Over the past few decades, new research and fossil recoveries have expanded the fossil hypodigm used to calculate the mean ECV of *H. erectus* s.l. (Abbate *et al.* 1998; Asfaw *et al.* 2002; Vekua *et al.* 2002; Baba *et al.* 2003; Macchiarelli *et al.* 2004; Potts *et al.* 2004; Spoor *et al.* 2005, 2007; Bauer & Harvati 2015; Rightmire *et al.* 2017). Some fossil *H. erectus* specimens on the smaller end of the hypodigm's ECV range now overlap with the upper range of *Homo habilis/rudolphensis* ECV (Spoor *et al.* 2007; Klein 2009; DeSilva 2011; Antón 2012; Isler & Schaik 2012; Bauer & Harvati 2015; Spoor *et al.* 2015). The Dmanisi, Georgia fossils have introduced the possibility that a small, and potentially more primitive group of hominins, could be included as early members *H. erectus,* could be closely related to *H. habilis,* could be a sub-species of *H. erectus* (*H. e. georgicus*), or could be the new species *Homo georgicus* (Lordkipanidze *et al.* 2006; Cela-Conde & Ayala 2007; Ferring *et al.* 2011; Lordkipanidze *et al.* 2013b; Zollikofer *et al.* 2014; Rightmire *et al.* 2017). Late surviving Indonesian *H. erectus* populations have ECV values well within *H. sapiens* lower ranges (Weidenreich 1943; Lestrel & Read 1973). Some consider the Late Indonesian fossils (e.g. Ngandong) to be a separate regional sub species, or feel the earlier classification of *Homo soloensis* should be revived for them (Weidenreich 1943; Widianto & Zeitoun 2003; Zeitoun *et al.* 2010). Note, however, that some Indonesian scholars are still using *Pithecanthropus* for the Javan fossil hominin specimens, dividing them into *P. erectus* and *P. soloensis* (Rudin & Jati 2021). This will be covered in more detail in Chapter 3. The fossil membership of *H. erectus* has expanded and contracted, changing our ideas about the hypodigm's ECV-, geographic-, and temporal range. If the new range/ means are used with the existing published regressions, how would the predictions change?

Additionally, histological research of fossil hominin teeth has produced a potentially much younger $M_1$Age for *H. erectus,* with a histology-estimated $M_1$Age of 4.4 yr for S7-37[3] and an $M_1$Age estimate (derived from the S7-37 estimate) of 4.0 yr for KNM-WT 15000 (Dean *et al.* 2001). That would be a shift of as much as -0.6 yr from previously published *H. erectus* $M_1$Age predictions. In light of the expansion of the *H. erectus* ECV range, this thesis revisits the effectiveness of the use of extant primate $M_1$Age and ECV regressions to predict fossil *Homo* species' $M_1$Age with a focus on *H. erectus*, using the S7-37 estimate as a test case.

As histologically derived $M_1$Age estimates for subfossil and fossil primates have been published, if fossil data points are added to the data set, how will that impact the accuracy of predictions? Do progressive taxonomic exclusions (e.g. Catarrhini-, Hominoidea-, or Hominidae-only) significantly change the performance of the predictions? Would using a different type of regression equation (e.g. quadratic or cubic regressions) change the performance of the

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[3] It would be prudent at this point to clarify that this histologically-derived $M_1$Age *is* an estimate. The histology calculates age at death from the neonatal line to the end of the developmental root. Age at eruption has been estimated by the amount of root length present. As understanding of extant ape root extension rates continues to evolve, revisiting estimated ages may, of course, lead to adjusted $M_1$Age estimates in future. The limitations of using age estimates from individuals (fossil or exant) where species means are not available is also important to keep in mind.

data set? Can any of the above permutations accurately predict hominin $M_1$Age? Can they do so without post-regression adjustments?

In order to provide the reader with an understanding of life history theory and related terms, as they are applied to human evolution, Chapter 2 will present and discuss life history concepts and terms in greater detail. As the taxonomy of *H. erectus* is still a matter of debate, Chapter 3 will discuss a working definition of *H. erectus* for this study. This will involve a discussion of the complicated varying taxonomies proposed, and related debates on the pattern of human evolution. It will also explore how the history of this debate and available fossil and archaeological evidence impacted upon past reconstructions. However, an exhaustive review of the taxonomy for *H. erectus*, and the other *Homo* species is outside of the scope of this thesis.

Chapter 4 will discuss the primate data used in the regression analysis, and cover some of the issues with data quality and availability. It will also provide an overview of the various regression methods used, and how I apply them to exploring the questions of this study. Chapter 5 presents the regression model results. Chapter 6 will then present the Fossil Hominin predicted $M_1$Age results of selected equations. Chapter 7 will discuss how those results answer the questions I have set. Chapter 8 will conclude with whether the effectiveness of this specific type of life history related variable regression is accurate when used to recreate fossil hominin life history patterns.

# Chapter 2

# Chapter 2 Primate Life History: Backgrounds

This chapter presents the research backgrounds for primate life history data and hypotheses (both human and non-human) and how these are applied to understanding the life history of fossil hominin species and the evolution of the human life history pattern. The chapter is followed by a further backgrounds chapter covering exploring the history of definitions of the species *H. erectus* sensu lato.

In Section 2.1, an overview of life history terms is given. Then in Section 2.2 non-human primate life history patterns are presented, followed by a description of what is known about human life history patterns in Section 2.3. Fossil hominin life history details are presented in Section 2.4.

By necessity, the discussion of non-human primates life histories will not be exhaustive, as that is outside the scope of this thesis. It will focus on patterns/ variables as relevant to the understanding of (or the contrast with) the human and fossil hominin life history patterns. Why the focus on human life history, isn't this study about fossil hominin life history? An outline where human life history is unique from non-human primates is needed because much of the discussion (and application) of predictions of fossil hominin life history variables and patterns centre on *when*, in our evolutionary lineage, the various aspects of human life history evolved. What we can estimate about fossil hominin patterns can be applied to questions about how human patterns came to be. At times the wording of some hominiod life history[4] reconstruction/description work tends to

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[4] as well as other traits

focus on how close a species' life history strategy or variables are to those of *Homo sapiens* versus extant hominids (i.e. having life history timing or patterns which are "human-like", "ape-like", "characteristic of...", "share a pattern with") (Smith 1986b; Conroy & Vannier 1991; McHenry 1992; Smith 1992; Hartwig-Scherer 1993; Smith & Tompkins 1995; Benyon *et al.* 1998; Dean 2000; Falk *et al.* 2000; Kelley & Smith 2003; Dean 2006; Monson *et al.* 2022; Berghänel *et al.* 2023).[5] This tendency may be linked to the historical tendency to attempt to define the "uniqueness" of human traits which differentiate humans from other primates specifically and other animals in general (Cartmill 1990). This would be in contrast, for instance, to works which challenge the notion of a marked difference between extant hominid life history patterns (Walker *et al.* 2018) or focus on the impact of both socio-ecological environment and neutral evolution on life history traits (Yim *et al.* 2023).

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[5] However, this practice should be differentiated from the use of "-like" when referring to the assumption of shared similarity in variation from the line of regression, in the practice of ad hoc adjustments to $M_1$Age predictions (Smith *et al.* 1995).

## Section 2.1 Life History Introduction

This section now presents an overview of life history theory and a definitions of life history terms employed in this text. Life history strategy refers to the pattern and timing of growth, reproductive maturity, and longevity of a species. This pattern evolves in response to the mortality schedules imposed by the environment (Purvis *et al.* 2002). An observable marker of life history strategy—such as gestation length, weaning age, age at first reproduction (hereafter **AFR**)[6], interbirth interval (hereafter **IBI**)—is referred to as a **life history variable** (hereafter **LHV**). As many LHVs are not directly observable in the fossil record, certain skeletal markers are studied as proxies in order to estimate the life history strategies of fossil species (Wood 2009). These skeletal markers are a type of **life history *related* variable** (hereafter **LHRV**): physical traits that highly correlate with life history variables, such as ECV and body size. Dental emergence timing is an LHV that has been seen as closely (if not directly) tied to weaning age (another LHV) in most primates. However, a direct 1:1 correlation between weaning and $M_1$ emergence is not supported in recent chimpanzee field studies (Smith *et al.* 2013).

Throughout their life cycle, organisms balance the energy output required for growth, survival, and reproduction in a way which reduces mortality while maximising fecundity within an ecological niche (Purvis *et al.* 2002; Wood 2009; Schwartz 2012). Within paleoanthropology, life history theory investigates

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[6] As a comparative LHV data point, the female age of first reproduction generally is recorded as the age at first birth

human evolution from this perspective of energetic balance. This allows for the exploration of the energetic drivers and constraints of the evolution of *Homo* species traits.

When estimating life history strategies of fossil hominins, the age of emergence of the lower first permanent molars can imply the pace of completion of pre-juvenile stage growth because it correlates with LHVs in extant primates (Harvey & Clutton-Brock 1985; Harvey *et al.* 1987; Smith 1989a, 1991a). Because dental emergence schedules are less reactive to environment than other skeletal markers, molar development has historically been seen to be a fairly reliable skeletal marker of life history in fossil hominins (Dean 2006). Relative brain size is 'read' in the fossil record through the measurement of the ECV of fossil skulls. Mean $M_1$Age is reported to be highly correlated to ECV in primates (Smith 1989a). Regression equations of ECV have been employed to predict possible mean $M_1$Ages for fossil hominin species (Smith *et al.* 1995). However, some extant hominid studies have identified body mass as the best predictor of life history events, and caution against inferences made from dental development (Robson & Wood 2008). However, other researchers have contested this and hold to the predictive value of primate dental emergence, positing other explanations for mismatch between age at death estimates for near-$M_1$ emergence fossil hominins and regression predicted fossil hominin $M_1$Age (Kelley & Schwartz 2012; Kelley & Bolter 2013).[7]

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[7] This debate on the predictive reliability of dental emergence for fossil hominins will be covered in Chapter 7 (Discussion).

In order to understand what details of *Homo erectus* s.l. life history could potentially be assessed by predicting $M_1$Age for the species, we will now turn our attention to extant primate life history patterns and how *H. sapiens* life history differs from that of non-human primates. The chapter will now give an overview of primate and human life history, before moving on to addressing the various regressions methods which have been employed to predict *H. erectus* life history strategies.

## Section 2.2 Primate Life History

What do primate life history strategies look like? As mammals, primates have comparatively long life spans and tend to produce—at long intervals—small litters of slow-growing offspring, which remain highly dependent until adulthood. Primates have some of the lowest mammalian rates of birth, growth, and mortality, in concert with brain growth rates which are higher than expected in contrast to their body growth (Kappeler *et al.* 2003). As eutherian mammals, primates provide the energy their offspring require for growth both prenatally to the foetus via some form of placenta, and postnatally via lactation (Bogin 1999b). Primate infants are generally at the more precocial end of the mammalian spectrum and the ancestral state for primates is singleton births (van Schaik & Isler 2012). However, primates do not have offspring that are highly precocial enough to follow their mother from birth, and therefore primate infant care strategies employ carrying, parking/nesting, allocare[8] or some combination of these behaviours (Ross 2003). While humans have evolved a high degree of allocare for infants, humans are the exception to the rule amongst extant hominids, where carrying is performed by allocarers for less than 5% of infant care time (Ross 2003).

Many mammals tend to have a life history pattern with growth stages which progress directly from infancy to adulthood. While there is a high degree of species variability within the order, the most highly social primate species display a juvenile growth stage 'inserted' between infancy and adulthood as would be

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8. allocare = care provided by individuals other than the mother

expected in highly social mammals—e.g. social carnivores, elephants, and some cetaceans (Bogin & Smith 1996; Bogin 1999a).

In mammals ECV highly correlates to longevity (Sacher 1978). ECV is correlated to many LHVs in the Primate order, and some of these LHVs appear to have a stronger positive correlation to ECV than longevity does (Harvey & Clutton-Brock 1985; Skinner & Wood 2006). In primates, ECV has been shown to be very highly correlated to $M_1$Age (Smith 1989a). A review of ECV, dental, and growth correlations has demonstrated that they are less reliable when applied at low-rank taxonomic levels, and that it is difficult the infer the presence of a childhood phase (for instance) based on adult ECV (Bermúdez de Castro *et al.* 2015).

There is a wide range of fast to slow life history patterns across the order Primates. Primate life history pace tends to scale with body size. The range starts with the smallest, *Microcebus murinus*, with an adult mass of just 65g. *M. murinus* sexually matures before 1 year and dies in the second or third year. At the opposite (slow) end of the Primate life history pace range is the 35,000g *Pongo abelli* which delay AFR until 15 years, displays IBIs greater than 8 years and a maximum recorded life span (hereafter life span) of 60 years (van Schaik & Isler 2012). However, life history pace isn't uniformly correlated to body size across primates, as there are many variations between species of similar body sizes (van Schaik & Isler 2012).

The relatively slower growth rates seen in primates reduce primate energy requirements, which improves their survival in environments which are punctuated with unpredictable periods of food scarcity (Bogin 1999b). Species with these slower life history patterns and relatively precocial infants are more likely to live in groups and have longer life spans. These longer life spans may contribute to primate life history plasticity by increasing the likelihood of that extreme condition events are experienced during individuals' lifetime (van Schaik & Isler 2012). The disadvantages of slow growth in group living species may be outweighed by the reduction in predation risk provided by group living and by delaying some of the foraging competition which can occur in large groups (Ross 2003). Most of the extant hominids[9] (excluding gorillas but including humans) grow more slowly than the primate average (Robson *et al.* 2006).

### Section 2.2.1 Primate Gestation, Birth, and Interbirth Interval

Primates tend to have relatively precocial infants compared to other mammals. This is in contrast with more altricial species, which generally have shorter gestation, smaller relative ECV at birth, larger litters, and faster postnatal growth (van Schaik & Isler 2012). All hominids have slow life histories, in (Robson & Wood 2008). Gorillas are especially significant amongst hominids for their absolutely larger body size paired with their relatively faster rates of growth (AFR = 10 years) and shorter IBIs (Robson *et al.* 2006). While *Pan*

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[9] **hominids** here refers to members of the Family Hominidae (great apes, humans, and fossil hominins) and **hominins** refers to members of the sub-tribe Hominina (humans, fossil humans, and australopiths). In this specific discussion of extant primate life history, hominids refers to the extant members of the Family Hominidae. **Australopiths** refer to the australopithecines, the non-*Homo* members of the sub-tribe Hominina (e.g. *Australopithecus*, *Paranthropus,* etc.).

*paniscus* (bonobos or “pygmy chimpanzees”) and *Pan troglodytes* (chimpanzees) have similar gestation lengths to each other, *P. paniscus* has somewhat lower adult and neonatal body weights, shorter lactation periods and interbirth intervals (van Schaik & Isler 2012).

IBI appears to be impacted by nutrition and environment variations in Colobinae, a number of Cercopithecinae, and some of the Hominidae—chimpanzees as well as humans (Struhsaker & Leland 1987). Amongst the non-human hominids, Mountain gorillas (*G. b. beringei*) have the shortest IBI (~3.9 yr) relative to female body mass and *Pongo* species have the absolutely longest IBIs at 7.8 to over 8 yr (Aiello *et al.* 1991; Robbins *et al.* 2004; Wich *et al.* 2004; Watts 2012). Wild *G. g. gorilla* and *G. g. beringei* have IBIs of 4-6 yr, although numbers of individuals observed are much lower (n < 9) than for *G. g. beringei* (n = 62), which have IBI mean of ~3.9 yr (Robbins *et al.* 2004). *P. troglodytes* has a mean of 4.4 yr IBI (range 2.9 to 7 yr) (De Lathouwers & Van Elsacker 2005); however other sources have reported *P. troglodytes at* ~5.6 yr and described this IBI as being are shorter than the IBI reported for modern human hunter-gatherers (Aiello *et al.* 1991; Watts 2012). Captive *P. paniscus* mean IBI is reported at 4.9 yr (range 1.9 to 7.6 yr) (De Lathouwers & Van Elsacker 2005). Captive *P. troglodytes* populations appear to have faster IBIs than wild *P. troglodytes* populations, while wild mountain gorillas and bonobos show little variation between captive and wild populations (Anderson *et al.* 2008).

Interestingly, wild populations of western lowland gorillas do, however, show more variation between wild and captive populations, linked to the greater unpredictability of food availability in the frugivorous lowland gorillas' environment (Stoinski *et al.* 2013). The apparent lack of plasticity in response to apparent nutritional abundance in bonobos and mountain gorillas may be connected to the their tendencies to rely on leafy vegetation when favoured foods are scarce in a way that *P. troglodytes* do not.

*Pongo* sp. diets are most similar in composition to *P. troglodytes* diets (Rodman & Mitani 1987). However, even in captive conditions with ample food and low energy outputs, *Pongo* species demonstrate longer IBIs than even humans living in conditions of high ecological stress (Anderson *et al.* 2008). *Pongo* sp. IBIs are lengthened in part due to their absolutely later ages of weaning, which is likely linked to their semi-solitary living patterns (Mikeliban *et al.* 2021). The longer IBIs of solitary roaming *Pongo*, therefore reflects the impact that allocare has on reducing IBIs within the group-living hominids (most dramatically expressed in humans). This is an example of how it would be inappropriate to assume a strictly linear trajectory between extant hominids and AMH life histories, onto which fossil hominins could be placed based on ECV: extant hominids life history variable can be quite different despite having similar ECV (*Pan* vs *Pongo*) or they can be fairly similar despite differences in ECV and body mass (*Pan* vs *Gorilla*).

### Section 2.2.2 Primate Infancy and Lactation

The milk composition of most primates is noted to have a relatively high amount of lactose. Relative to other mammals, primate milk tends to be more diluted as befits species who carry their infants and provide frequent and short bouts of "on demand" nursing (van Noordwijk 2012). In *G. gorilla*, infants suckle at least once an hour for the first 18 months, gradually reducing bouts to under 0.5 bouts/hour, with age (Stewart 1988). Most primate milk—with the exception of some "nesting/parking" species within the Strepsirrhines—has a high lactose content and lower fat and protein content. Lactose provides the high energy requirements of postnatal growth of primate brains (van Noordwijk 2012).

Weaning age is an important life history variable which appears to correlate with other LHV and LHRVs. What is known about primate weaning ages? hominids wean at a point when they are developed enough to digest solid food and forage competently, but they may still receive carrying and rely on "umbrella care" provided by their mother, in-group, or (step-)siblings throughout their juvenile stage (van Noordwijk 2012). *G. gorilla* infants have been observed to continue suckling into the 40-44 month age range (Stewart 1988). With the latest weaning age of primates, at 6.5 to 9 yr, *Pongo* species are one of the mammals with the longest periods of nutritional dependence (Mikeliban *et al.* 2021).

Before suckling ceases, infants may begin eating foods. This behaviour is referred to as complementary feeding (hereafter **CF**). In general, hominid infants begin CF at a relatively larger body size relative to birth weight (hereafter **BW**) than human infants, which start CF at 2.1× BW The hominid  range, starts from from 4.9 × BW in *P. troglodytes* up to 9.4 x BW in *G. gorilla* (Bogin 1999b). In *Pongo,* this absolutely longer period of nursing/nutritional dependence is important to immatures attaining food processing skills from their mothers, which is thought to be linked to their semi-solitary living patterns (Mikeliban *et al.* 2021).

For Primates, ratio for weaning age to gestation length is reported to be 1.63. However, it should be noted that the range of variation between primate species is so wide that this ratio has been described as being virtually meaningless (Dettwyler 1995). For all large bodied primates the time between birth and weaning is longer than the time for gestation, and for the hominids it is more than 4 to 6 times longer than gestation (Harvey & Clutton-Brock 1985; Dettwyler 1995).

Primate-wide, LHVs are correlated to dental development. Weaning in most primates has been thought to directly coincide with $M_1$Age, and has been demonstrated to be highly correlated to $M_1$Age (Smith 1989a, 1991a, b, 1992; Smith *et al.* 1995). However, the value of this correlation for predicting weaning age has been shown to be more tenuous when comparing closely related hominoids (Dirks & Bowman 2007; Robson & Wood 2008; Guatelli-Steinberg 2009; Humphrey 2010). Weaning has been seen to predate $M_1$Age in *Pan* and some evidence suggest it may also do so within the hominin clade more generally (Skinner & Wood 2006; Smith *et al.* 2013). Despite significant life history strategy differences, both humans and chimpanzees (*Pan troglodytes*) maintain a close temporal association between several dental eruption events to the completion of brain size growth and sexual maturity (Smith & Tompkins 1995).

For non-human primates, $M_1$Age corresponds to the age at which 90% of brain volume growth has been completed (Schwartz & Dean 2000). In *G. gorilla,* one study noted that suckling could continue into the first month of the mother's subsequent pregnancy, but of limited observations, no suckling was noted after that first month (Stewart 1988).

Weaning age (i.e. end of lactation) can be difficult to pinpoint because the transition to being fully weaned can be a gradual process (van Schaik & Isler 2012). In hominids, dietary supplementation alongside nursing can predate weaning by a number of years (Skinner & Wood 2006). As weaning age can be difficult to pinpoint during field studies of longer lived primates, weaning age may not always be published for a given species/subspecies, or may be based on a very small number of mother/infant dyads. Historically, researchers have published estimated weaning ages calculated from subtracting gestation from IBI, which will tend to underestimate lactation length as infants in some species can suckle during or throughout a mother's subsequent gestation (van Schaik & Isler 2012).

An important factor of primate infancy and group fitness is **allocare**. Allocare improves group fitness by reducing maternal reproductive energy costs and IBIs, by better provisioning immatures, and by improving care skills of pre-reproductive allocarers (Lonsdorf & Ross 2012). Allocare in hominid mother-infant dyads and dependent juveniles can reduce the mother's reproductive energy costs, increase offspring fitness, and increase the parenting skills of the allocarers (Lonsdorf & Ross 2012). In terms of direct care (defined by time observed infant carrying), there are many New World Monkey species are known to employ an allocare strategy (Ross 2003). However, in non-human hominids, infant allocare happens at a very low percentage of care, with no non-human hominid allocarers providing more than 5% of infant care (Ross 2003).

Direct paternal care is rare across the primate order, and the only ape which displays direct paternal care is *S. syndactulus*, where after the first year, fathers do most of the carrying (Lonsdorf & Ross 2012). Amongst *G. gorilla*, immatures are observed to be attracted to interacting with the dominant silverback and orphaned juveniles may treat them as their primary caretakers (Lonsdorf & Ross 2012). The semi-solitary *Pongo* species have the longest weaning ages and IBIs, and immatures must have gained full foraging skill set from their mother before weaning as they range independently shortly after (Mikeliban *et al.* 2021). Indirectly, mother-infant pairs can benefit from association with male "friends" and male-infant indirect interactions can be positive, neutral, or negative (Lonsdorf & Ross 2012).

Mothers and infants may also benefit from foods provisioned by other group members. Food sharing is often cited as a unique human trait, but many primatologists note evidence of food sharing in other species. Food sharing in non-human primates can generally be described as either solicited by immatures (via begging) or permitted "theft" of foods that adults are eating. For example, while *P. abelii* immatures solicit their mothers for foods they are not yet skilled enough to process themselves, only 1% of observed food solicitation events are initiated spontaneously by the mother (Mikeliban *et al.* 2021). It would be more accurate, perhaps to classify as unique the human trait of sharing to as degree at which sharing reaches the level of innate compulsive *gifting*. More specifically, it should be considered as part of the suite of traits which comprise the human cooperative breeding strategy, and this will be discussed in more detail in Section 2.3.1.A.

### Section 2.2.3 Primate juvenile Growth Stages

While many mammals essentially lack a growth stage between weaning and sexual maturity(and nutritional independence), many higher primates have a juvenile growth stage between weaning and adulthood, during which somatic growth is slow and they gain experience needed for social and biological survival (Kappeler *et al.* 2003). While infants are fully dependent on their mother for nutrition, juvenile individuals have weaned and have begun attaining enough adult dentition to consume foods which they have started self-provisioning—supplemented by mothers and other adult group members (Bogin 1999b; van Noordwijk 2012).

There is variation in the presence and length of juvenile stages across primates. For instance, the length of the juvenile stage in primates is robustly correlated with absolute adult brain size (Ross 2003). One primate which follows a common mammalian growth curve is *Callithrix jacchus*, where neonatally growth curve acceleration is followed by a deceleration before birth (Bogin 1999b). They don't appear to have a juvenile growth stage and sexual maturity is attained around 15-24 months. Colobus monkeys represent an indeterminate juvenile growth pattern with a postnatal growth spurt that then declines in velocity until adulthood (Bogin 1999b). At the other end of the spectrum, baboons also reach peak growth before birth, but growth doesn't decline until the juvenile phase. Males have a weight GS, which isn't demonstrated in females (Bogin 1999b).

For most haplorrhine primates, there is a juvenile stage, which is a period of non-reproductive independence which allows for intergenerational socialisation and facilitates the development of sex-typical behaviours and complex social relationships (Kappeler *et al.* 2003). The length of the juvenile stage is robustly correlated to absolute adult brain size suggesting that large brains do impose energetic constraints on rates of somatic growth (Ross 2003).

Although juveniles aren't as dependent on their mothers as infants are, the impact of maternal care for a juvenile offspring's overall development remains significant. For instance, whilst it is common for orphaned juveniles to survive their mother's death (where infants would not), those that do survive to adulthood go on to demonstrate a variety of social and physiological deficits which can often be passed on to their own offspring and create intergenerational deficits in early mothering skills (Lonsdorf & Ross 2012; van Noordwijk 2012). Notably among mammalian orders, primates may display maternal support throughout the mother's lifetime and may even expand to grand-offspring (van Noordwijk 2012). With the exception of the semi-solitary *Pongo*, in diurnal primates "stacking" at least 2 immature offspring (i.e. one infant and one dependent immature) at any given time appears to be the "rule" (van Noordwijk 2012).

During the juvenile phase, hominids will acquire the full suite of foraging, tool use, and food processing skills of their mother, but male-specific skills (such as *P. troglodytes* with hunting) may develop only from adolescence onwards (van Noordwijk 2012). In *Pongo* species, however, their semi-solitary social pattern means that they cannot rely upon association partners' knowledge: their acquisition of foraging skills is acquired by observing their mothers, and must occur before they start ranging independently, shortly after they are weaned (Mikeliban *et al.* 2021).

### Section 2.2.4 Primate Adolescent Growth Stages

Adolescent growth stage timing can vary sexually dimorphically within a species and growth spurts may differ accordingly. Humans are noted for our low levels of sexual dimorphism. Sexual dimorphism is also relatively low in *Pan*, with chimpanzee and bonobo males being only 30% heavier than females (Nishida &

Hiraiwa-Hasegawa 1987). Female gorillas reach first oestrus at about 7.5 yr and AFR at 10 yr (Stewart & Harcourt 1987).

Much has been made over whether human's are unique with regard to possessing adolescent growth spurts, with an emphasis on skeletal/length growth spurts. Some point out that this ignores the many other large anthropoids are who are slow-developing social primates that also demonstrate periods of rapid growth acceleration (Pereira & Leigh 2002; Kappeler *et al.* 2003; Weisfeld 2006). Very recently, researchers employing non invasive limb measurement and urine collection techniques with captive *Pan paniscus* demonstrated the presence of both length and weight GS in that species (Berghänel *et al.* 2023). Historically the discussion of linear (skeletal) GS in humans has downplayed weight GS observed in other primates. Berghänel *et al.* (2023) emphasise the importance of applying correct scaling and note that the previously reported apparent absence of this trait can be an artefact of incorrect scaling. Those who see the human skeletal GS as unique tend to emphasise the relative degree and specific timing of the human skeletal growth spurt (as addressed in Section 2.3.1.D). However, the use of bio-markers (Berghänel *et al.* 2023) may improve hominid cross-species GS comparisons in future.

### Section 2.2.5 Primate Ovarian Cycles & Reproductive Senescence

Amongst extant hominids there is considerable variability in the level of physical signs displayed during the peri-ovulatory phase. However, across the hominids, the mean lengths of ovulatory cycles tend to be fairly similar (averaging ~30.5 days across the 4 genera), suggesting that many reproductive traits have been preserved amongst hominids (Durgavich *et al.* 2023).

Reproductive senescence occurs at approximately the same age for all extant hominids (including humans). Therefore, human post-menopausal survival is not a factor of earlier reproductive senescence, but appears to result from selection for relatively slower rates of somatic aging (Robson *et al.* 2006). However, while ending fertility at similar timings, human fertility begins to decline about a decade earlier than in *P. troglodytes* (Hawkes *et al.* 2009). Human menopause will be discussed in greater detail in Section 2.3.

### Section 2.2.6 Primate Life History Data Issues

It should be noted that while primates have been studied extensively enough for the field to have a number of primate specific journals, primate species have not been uniformly sampled, and there are many large gaps in the knowledge base for the order. This is not necessarily a life history specific issue. For instance: recently the lack of evidence base needed for effective primate conservation has been urgently noted in a call to action (Junker *et al.* 2020).

From a life history correlation perspective, even in generally well described primate species, precisely *which* variables described is not uniform, and there are few species for which all LHVs and LHRVs have been described. In the larger and longer lived species, documenting some LHVs, has historically been hampered by short time-frames of field studies relative to LHVs with longer intervals such as IBI, and a lack of cross-troop longitudinal studies in species who migrate before sexual maturity can be observed (Rodman & Mitani 1987; Struhsaker & Leland 1987). Another example of non-uniformity of reported LHVs across Primates, historically, is the key primate-wide life history comparison study which described 14 LH variables for 139 primate species across 55 of the 56 known genera at the time (Harvey *et al.* 1987). In this historically widely cited study, only 6 species had complete data reported for all of the 14 variables: *Callithrix jacchus*; *Callimico goeldii*; *Hylobates lar*; *Pongo pygmaeus*; *Pan troglodytes*; *Gorilla gorilla*. Gestation age was available for 75 species; weaning age for 47; interbirth interval for 62; neonatal brain weight for 27 (Harvey *et al.* 1987). Female age at sexual maturity was paired with age at first breeding data in only 35 species (Harvey *et al.* 1987). This example is *historical*, and there have been updates/improvements to the available primate life history data. However care must be taken when compiling primate data that the current primate sources one relies upon have done the due diligence in their own sourcing and are not relying on any referencing chain whose origins rely on (or have not identified the use of) older sources in which the data may not have been as accurately transcribed.

In a more recent explorations of primate life history patterns, which only included species with no missing values for the variables discussed, only 87 primate species had sufficient matching variables to warrant inclusion (van Schaik & Isler 2012). They acknowledge that there will always be issues with data quality due to the vary nature of LHV species means, which are necessarily distilled from demographic data and can vary by individual, population, or temporal/environmental conditions. Some issues they highlighted in collating data from published sources include the historical use of weaning age (end of lactation) calculated from IBI minus gestation and female AFR calculated from age of sexual maturity plus gestation. Both tend to generate underestimated variables (van Schaik & Isler 2012). Having less represented species sampled does not necessarily interfere with studies which specifically seek to understand the broader trend across the Primate order, as it may be more appropriate to compare data at the family or subfamily levels (Harvey *et al.* 1987). An accurate generalisation for the order as a whole may not necessarily provide the level of comparative detail needed when comparing species within a family (e.g. Hominoidea), determining which LH traits are divergent in timing or degree in *Homo* species, or predicting LHVs in fossil hominins.

More generally, issues with conflicting interests between disciplines mean that not all published data can be applied to some study designs (e.g. primate behaviour to improve conservation; human data for medical applications; data needed for prediction of fossil hominin traits). There may be working definitions which do not match (e.g. weaning) and therefore the published variables or behaviours are not necessarily describing the same things. Additionally, studies which observe one quantifiable trait do not tend to simultaneously collect a matching trait and therefore the way in which traits covary at individual or population level cannot be directly assessed.

There is a degree of species bias, as much more data has been recorded for species historically used in laboratory research, for hominids as our closest relatives, and for species favoured by zoos or by researchers/projects with a strong popular culture profile. Even amongst the hominids, however, the numbers of individuals included in some studies remain low. For instance, a study of ovarian cycles in *Pongo sp.* was able to collect data for 98 cycles, but this was compiled from 6 individual females: 1 from each species of *Pongo,* as well as 4 hybrid individuals (Durgavich *et al.* 2023). Cycle lengths varied between and within individuals studied, while averaging near the hominoid mean.

While humans are equally related to both chimpanzees and bonobos, the latter have been frequently overlooked and understudied, despite being temperamentally more similar to humans (Hrdy 2009). Historically, a preoccupation with aggression and competition have meant that the violence-prone temperaments of primates such as chimpanzees have been projected onto human ancestors. While chimpanzees were recognised and described as a genus in the first half of the 19th century, bonobos were not described until 1929 (as a sub specific) and not fully classified as a unique species until 1954 (Napier & Napier 1967). The lack of research focus on bonobos has meant that there is no published $M_1$Age data available to allow them to be included in this study's regression equation, for instance. It is difficult to compare LH patterns of our two genetically closest relatives because bonobos have historically not been as well studied/reported as chimpanzees. In Nishida and Hiraiwa-Hasegawa's (1987) Primate Societies study, the LHVs reported for bonobos were listed as estimates, compared with the firm data reported for chimpanzees, with some values were still missing entirely. In a more recent follow up to this volume, The Evolution of Primate Societies, one study does now list data for some those comparative LHVs for bonobos (van Schaik & Isler 2012).

## Section 2.3 Human Life History

With the general pattern of primate life histories in mind—relatively larger brains with relatively slower growth *as mammals*, lower skeletal growth rates *as mammals*, a tendency towards singleton births or small litter-sizes, and relatively lower rates of reproduction and mortality *as mammals*—this section will now look at modern human life history within a primate context.[10] This section will present aspects of human life history: the longest maximum life spans of primates; a mixture of delayed maturation, extension of growth periods, prolongation of brain growth rates; a relatively reduced brain size at birth; the insertion of additional development stages; a propensity for cooperative breeding and ability the access cooperative lactation; and shortened interbirth intervals mediated by the ability to "stack" pre-juvenile offspring.[11] As primates, human gestation length is consistent with expectations, human body *mass* growth spurts are consistent for our size, and human later growth stages are within or reduced from expected, however human early growth stages are markedly extended (Leigh 2001). Like other social mammals, humans have a juvenile phase delaying sexual maturity and adulthood. Three additional life stages are also observed: **childhood**, a post-nursing stage of continued high rates of brain growth, highly specialised energetic and dietary needs, and dependence on other for food and protection (Bogin & Smith 1996; Bogin 1997, 1999a, b, 2009);

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[10] e. g. relative to other primates, and especially to other hominids

[11] "Stacking" has historically been used to refer to the human ability to support a new infant while still caring for and provisioning an existing pre-juvenile offspring, allowing for shorter interbirth intervals relative to our extended growth rates. It should be noted that other primates provide support to a juvenile offspring alongside an infant, and at times "stacking" is used to refer to this reproductive strategy as well.

**adolescence** with a sexually dimorphic skeletal growth spurt; and **menopause**, the female post-reproductive stage. The addition of these phases, the absolute longevity and slow life history of humans, the deviation from hominid patterns in both shortened interbirth intervals, relatively earlier weaning, and vigorous female post-reproductive longevity are seen as derived traits (amongst others) in humans (Robson *et al.* 2006). Some authors emphasise the impact of the shift to a human diet (which is energetically specialised for nutrient dense food "packages"[12]) is highly interwoven with life history evolution. It is proposed that the evolution of the human life history suite would have happened response to a broad and flexible enough set of food package procurement behaviours to permit habitation of a global range of habitats, and was specialised towards the brain complexity that allows for the acquisition of learned skills and knowledge which contribute to high rates of productivity later in life (Kaplan *et al.* 2000). There is debate over which human life history variables are unique or derived, which LHV to LHRV correlations produce useful predictions for hominins, etc. Nonetheless, the aim in life history regressions for fossil hominins is to predict the presence (or degree) of these human LHVs in their life histories and to better understand how and when those traits evolved. This section will introduce and break down these human life history variables, touching on some of the history of hypotheses regarding which are actually derived traits and on the evolution of human life history.

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12. "packages" here refers to individual food items which provide a large amount of nutrients (such as tubers and larger animals) as opposed to small items which need large amounts to be consumed to receive the same amount of nutrients (such as insects and berries).

### Section 2.3.1.A Human Gestation and Infancy

The general pattern for Primates is to have small litter sizes, lower rates of reproduction, and larger brains with faster growth rates. Humans tend to have singleton births, extension of growth rates, and a shorter interbirth interval. The shorter gestation and shorter interbirth interval than expected for adult brain size are partially due to human neonates being born at a reduced state of development than would be expected for an ape of our size. Note, however, that human gestation is within expectations for adult body size as primates (Leigh 2001)..

Humans are said to be **secondarily altricial:** while human neonates are **precocial** in other aspects of development, they are born the least neurologically and behaviourally developed of any primate (Zollikofer & Ponce de Leon 2010; Dunsworth *et al.* 2012). Human neonatal ECV is proportionally small, relative to adult ECV compared to non-human apes (DeSilva & Lesnik 2006, 2008). The proportionally smaller human neonatal brain is not uniformly underdeveloped: the subcortical portions are relatively mature at birth, while the neocortex is relatively immature and develops relatively slowly (Trevathan 1987).

The relatively underdeveloped neonatal brains and humans reduced gestation length has long been thought to have been directly constrained obstetrically: an optimal bipedal pelvis structure creates an upper limit for neonatal ECV. In-utero restrictions body weight can be seen in a reduction of growth rates at 34-36 weeks in utero. This slowing happens earlier in twin gestation, when the combined weight of the neonates is approximately the same as a 36-week singleton foetus (Tanner 1990). Tanner also notes that women of smaller stature (especially when mediated by a mother's own childhood malnutrition) tend to have lower birth weight babies. Tanner highlighted cross-species examples of maternal size restrictions on birth size. Conversely, it has been suggested that the hominin development of bipedalism, in reducing both predation pressure and intraspecific aggression, allowed for the slower growth rates necessary for the development of larger brains (Jablonski *et al.* 2002). If bipedalism was responsible for increased survivorship, then one could see the narrower bipedal pelvic outlet as both restricting neonatal ECV and allowing for the reduced fertility trade-off that extended development periods and delayed female AFRs represent.

More recently, however, the balance of maternal and infant growth energetics has been demonstrated to determine the initiation parturition in humans (Dunsworth *et al.* 2012). That is, despite their proportionally smaller ECV, human neonates bodies are absolutely larger. This reflects a greater maternal energetic investment during gestation, and total maternal energy input is finite. While it is true that pelvic morphology and increased encephalisation can contribute to parturitional complications, energetics pose the main constraint on human gestation length (Dunsworth *et al.* 2012). Reduced development at birth is not reserved to ECV, as many systems are not fully developed neonatally, such as the liver and the kidneys, which take weeks to months to develop full functionality (Trevathan 1987).

Due to this reduced level of development at birth, humans infants experience relatively higher neonatal growth rates relative to body size (Cofran 2017). This growth rate accelerates prior to parturition and extends postnatally into the first 1.5 yr of life (Cofran 2017). The many incomplete physiological and biochemical processes for normal function present at birth, and the continuation of prenatal-like growth rates means the human neonate can be conceptualised as an "exterogestate fetus" (Trevathan 1987). This extended period of neonatal development has popularised of the concept of the "Fourth Trimester"—the health/development stage represented by the first three postnatal months for the maternal-infant dyad—in sociology, medical, and legal discussions of maternal and infant health (Jennings & Edmundson 1980; Matambanadzo 2014; Montgomery & Laury 2019). While 3 months postnatally is seen as an underestimation of this stage, the Fourth Trimester perspective acknowledges the physiological & psychological trade offs for the mother required for providing for the higher dependence needs of a relatively less developed human neonate (Tully & Ball 2018).

Lower neonatal ECV and the extended postnatal brain growth period results in the human brain doing most of it's developing within an "enhanced environment" outside of the womb (Monson *et al.* 2022). This postnatal growth both increases energetic demands to accommodate expanded growth rates and enables the cultural complexity that allows human groups to meet these provisioning requirements (Cofran 2017). Therefore, related cranial variables in fossil *Homo* species which indicate the presence or absence of secondary altriciality have been a proxy for determining the linguistic and cognitive complexity of those populations.

Understanding lactation is key to the discussion of human infant development, infant survival, and group reproductive rates. It's impact on other stages, such as the insertion of a childhood phase, will be discussed in subsequent sections. Here I will address the difficulty in defining length of the human dyad's lactation/suckling period and it's role in gestation and infancy. From a life history timing lens, most notable—both in terms of examining exactly how humans differ from other primates and in terms of the difficulty of nailing down a "biological norm"—is the amount of quantitative and qualitative intraspecific variability in human breastfeeding initiation and weaning age. Discussions of nursing within primate life history have tended to focus on timings which can be used in calculations (e.g. IBI, reproductive capacity, etc.) or LHRV correlations. Increasingly, recent biological and cultural anthropology have emphasised the importance of studying the social, immunological, and developmental aspects of human lactation and breastfeeding. Human lactation is remarkable in it's flexibility (Palmquist 2018). This flexibility of cultural practices creates variations in maternal decisions around the initiation or length of their lactation. Human lactational flexibility is one part of what makes a species mean age of weaning harder to define for humans.

It is important here to acknowledge that within paleoanthropology (and the other anthropological disciplines) there has been a historical and continued lack of focus on breastfeeding and other aspects of reproduction in humans in what is published in the fields of anthropology and primatology. This is a result of men's domination of these fields during their early histories and men's lack of interest in these topics, as well as being linked to the impact of men's lack of access to aspects of women's lives (Stuart-Macadam 1995; Tomori *et al.* 2018). Additionally, the historical focus on primate evidence/models of aggression, war, hunting, and resource competition has distracted from focusing on what may be more unique human traits: cooperative breeding and sharing that reaches the level of "chronic readiness" to give gift and exchange favours (Hrdy 2009). Even with the impact of ethnographic pioneers such as Margaret Mead and an increase of interest in the breastfeeding, there remained a distinct lack of published studies in anthropological journals and ethnographic monographs well into the mid-2000s (Tomori *et al.* 2018). This is mirrored in medical research, where the funding into health benefits/costs of long term nursing within Western industrialised societies has historically been limited, and where few studies included categories for breastfeeding beyond 12 months (Lawrence 1995).[13] So while factors such as age of weaning in humans are already difficult to pin down because of the variations in cultural practices mediating breastfeeding, the relative lack of published research further complicates the issue.

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[13] However each study noted by Lawrence (1995)Lawrence (1995) demonstrated increasing dose-response benefits during the times that were studied.

So how then does one define mean ‘weaning’ age for humans? The WHO has made recommendations that help to synopsize human-wide biological minimums for avoiding negative maternal and infant health outcomes: exclusive breastfeeding for the first 6 months, at which age the introduction of  alongside continued breastfeeding to a minimum age of 2 yr (Martin 2018). Human infants—born without immunity—acquire an immune system via milk through a synergistic system of feedback between mothers, infant, and environment which alters the composition of the milk that provides a collaborative immunity (Miller 2018). The impact of this immunity is seen the negative infant health outcomes reported within cultures/environments with early weaning, early complementary feeding, and reduced initiation of breastfeeding (Martin 2018).

Breastfeeding benefits the mother over her and her offsprings’ lifetimes. A woman’s breast cancer risk can be reduced both by having been breastfed in infancy and by prolonged lactation with her own dependents (Micozzi 1995). Within the range of variability in timing of weaning cross-culturally, there is ample evidence that non-initiation of breastfeeding or weaning before 2 yr of age are associated with negative maternal and infant health outcomes—even in societies where milk substitutes are the norm (Cunningham 1995; McKenna & Bernshaw 1995; Stuart-Macadam 1995; Martin 2018). The multiple levels of health mediations that longer nursing provides indicates that human infants have a biology which evolved to expect a certain level of “continuous input from the numerous bioactive factors in maternal milk” to two years or more (Martin 2018).

Another impact on the study of the timing of weaning is the variation of the meaning of the word when applied in different subfields. Life history regressions have focussed on the timing of cessation of weaning when comparing primates. Weaning is a very slippery term and can refer to the initiation of , the cessation of all suckling, or to the transitional phase between these two points. In non-human primates ‘weaning’ is generally is used to refer to the end of the nursing relationship, which is correlated to dental emergence schedules and transitions to juvenile or adult stages in many primates. However, humans are not the only primate to only primate to have periods of mixed feeding, and recent research has indicated that dental LHRVs, such as $M_1$Age, aren’t directly tied to the end of suckling in chimpanzees (Smith *et al.* 2013). Some cross-species studies have defined ‘weaning’ as the age at which reconception takes place. This definition is inappropriately applied in primates, where low-level suckling frequently is observed to continue through to the mother’s subsequent parturition (Dettwyler 1995).

Using the definition of weaning as the cessation of nursing then, and taking the WHO minimum age of 2 yr into account, what is the accepted age of weaning for humans? Cross-cultural reports from a wide range of of non-dairying cultures indicate a window of between 2 and 5 yr, and a widely accepted average of between 3 and 4 yr, (Dettwyler 1995; Stuart-Macadam 1995). Age of weaning is also an interplay between infant and mother, with it being noted ethnographically that weaning before the age of 4 is rarely child-initiated (Dettwyler 1995). In modern human groups known to be ancestrally non-dairying, with limited gene flow exposure with European populations, the age at which lactose tolerance declines has been used a a proxy for a human weaning age, with a mean age of 3 yr (Stuart-Macadam 1995). So 3.5 yr ±0.5 seems to be the most appropriate mean age.

At 3 to 4 yr, human weaning age happens before infants are capable of independent feeding and occurs earlier than expected for their age at maturity (Robson *et al.* 2006). In humans, at the age of weaning, neither the digestive system nor dentition is mature enough to process adult foods (Thompson & Nelson 2011).

The impact of extended neonatal dependency is often mediated by other factors in human life history and human culture. Humans have a propensity for cooperative breeding (Palmquist 2018). Humans are unique among primates in the absolute degree of flexibility around the mixed feeding stage (Martin 2018). Humans are unique in the ability of infants to survive after the death, absence, or inability to lactate of the birthing parent. This is part of human cooperative lactation: the full range of strategies to provide infants with milk which include someone other than a birthing parent (Palmquist 2018). This is not just through the infant’s ability to access milk outside it’s birth dyad—eg through wet-nursing, co-nursing, cross-nursing, expressed milk, shared milk and milk substitutes.

Humans are also capable of non-puerperal lactation through either induced lactation or relactation— which has been reported historically and ethnographically as being practiced by co-parents, grandmothers, and adoptive parents (Palmquist 2018).

Additionally, as we will see below, human longevity and menopause are uniquely human, meaning humans females live beyond the cessation of ovulation. This means that we can also observe the extensions in the length of the mixed feeding stage (and the nursing relationship) in mother's last offspring, which are widely reported to extend well beyond the average cessation of nursing age in many cultures (Dettwyler 1995). This highlights the interplay between the push and pull factors determining length of the breastfeeding relationshi*p.* The pull factors are the biological, social, emotional, developmental, and immune benefits of the extension of suckling. The push factors are the negative impacts that the extension of lactation on maternal energy and maternal fertility rates. The next section will now address the other unique human life history stages which are tied to human secondary altriciality and the energetic requirements of the growth and maintenance of the uniquely large human brain.

### Section 2.3.1.B Human Childhood

Humans, as social mammals, demonstrate an extended period of growth between infancy and adulthood through a juvenile stage. Human early growth stages are markedly extended from that expected for primates based on body mass (Leigh 2001). Humans have inserted phases on either side of the juvenile growth stage: childhood and adolescence (Bogin 1999b). The childhood phase accounts for a good deal of the extension of human ontogeny. This section will define and address the human childhood phase.

While human brain growth rates are absolutely high in infancy, the achievement of adult brain size is slow, and human sexual maturation is delayed (Zollikofer *et al.* 2014). Delayed growth rates should result in more significantly reduced fertility rates than are actually observed in humans. As has been discussed above, in highly social primates weaning generally marks the attainment of relatively greater dental and physical maturity than seen in human infants. Weaning in higher level primates usually coincides with the start of the juvenile growth stage. Juvenile growth stages are associated with the ability of self-provisioning in which the mother is able to support a subsequent offspring/ litter. Humans at the age of weaning are significantly underdeveloped relative to that stage.

The average human weaning age (within non-dairying societies) is 3±1 years of age rather than the ~7 yr which would be expected if human life history variables met the pace expected for non-human primates correlated to mean adult ECV (Dettwyler 1995).[14] Human childhood consists of a uniquely early pre-juvenile post-weaning phase of continued dependancy paired with a maternal return to producing subsequent offspring. This uniquely human practice of initiating early reproduction and caring for a new infant, while still maintaining a dependent offspring has been referred to as "stacking" dependents (Robson *et al.* 2006). Because early weaning allows for a shorter interbirth interval (IBI), it makes up for the deficit in fertility caused by delayed initiation of the reproductive stage. As such, the childhood phase can be viewed as balancing the deficits of delayed sexual maturation with the "catch-up" of early weaning (Zollikofer *et al.* 2014).

Indeed, human brains are absolutely large relative to our gut size. While non-human simian primates have an EQ of 1.9, human EQ[15] is 4.6 with a brain that is 1.04kg larger than expected for a mammal of our size, while the mass of the human splanchnic organs is 900g less than expected without any significant increase in BMR[16] (Aiello & Wheeler 1995). In addition to human's relatively reduced gut, humans have a different gut structure (with small intestine 56% of total gut structure and a decreased colon) compare to the non-human apes (small intestine is 14-29% of gut); making humans similar in proportions to other mammals which also demonstrate an increased energy requirement

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[14] Weaning in this context is used to refer to the absolute cessation of suckling, rather than the introduction of provisioned foods and the period of gradual increase in provisioned energy and decrease of suckling. The biological norm for the introduction of provisioned energy in human infants (excluding the use of milk substitutes) is 6 months.

[15] EQ (encephalisation quotient) is the ratio of observed brain mass to expected brain mass for placental mammals based on body mass.

[16] basal metabolic rate

without a decrease in diet quality (Milton 1986). This gut reduction, proportional restructuring, and shift to higher quality diet is thought to have allowed for increased brain size evolution (Aiello & Wheeler 1995). The maintenance and, especially, growth of the human brain is highly energetically demanding, especially relative to the time available for digestion of food within the gut. When body mass is controlled for, there is a positive correlation between improved diet quality and increased encephalisation (Fish & Lockwood 2003). Human diets are necessarily highly nutrient dense, and the acquisition of these foods demands complex socioenvironmental skill sets which takes longer periods of learning during growth to acquire (Bogin 1999b).

The human childhood phase can be seen as an artefact of the energetic demands growing of human brains. Humans wean and transition into childhood before the digestive system and dentition have matured enough to process adult foods (Bogin 1999b; Thompson & Nelson 2011). Following weaning, human brain growth and delayed maturity necessitates a longer period of time before transitioning to juvenile growth and juvenile levels of self-provisioning. Because of this immature gut development, human children must meet the energetic requirements of brain growth through a more easily digestible and highly energy and nutrient dense diet (i.e. specialised), which requires a great degree of social complexity and allocare to provision (Bogin 1999b). This specialist diet and high energy demands mean that increasing fertility through earlier weaning is only viable through **alloparental** care/provisioning (Zollikofer *et al.* 2014). Thus childhood can be seen as both a feeding adaptation and a reproductive adaptation (Bogin 1999b).

The importance of human cooperative breeding behaviours and active resource provisioning cannot be overstated here. While other hominids may tolerate theft or respond to begging from infants, friends or allies, they do not exhibit the spontaneous giving/sharing impulses of humans which are observed in even very young human children (Hrdy 2009). In non-human animals, the levels of voluntarily offering preferred food gifts are only seen in highly social species with deep histories of cooperative breeding (Hrdy 2009). Other highly social, cooperative breeding species are similarly known for secondarily altricial offspring.

Human pre-juvenile body growth is slowed compared to brain growth. The energetic demands of brain growth are offset by delayed physical and sexual maturation, reducing the total caloric burden of provisioning for non-nursing dependents (Bogin 1999b). This advance cognitive growth relative to maturation means that juveniles, while self-provisioning and consuming a less specialised diet, can also provide allocare to children in the grou*p.* Juvenile (alongside adolescent and adult) members of the group help mothers provision, care for, and protect children (Bogin 1999b). This facilitates the maintenance of multiple energetically demanding offspring that require slow growth for the acquisition complex survival skills (Bogin 1999b).

It should be noted that there is significant intra-specific variation in birth spacing and the degree of children's contribution to subsistence, as these are partly facultative adaptations (Konner 2005). The attention to nursing, weaning, parental and alloparental care, birth spacing, etc has been historically sparse and is complicated both by taboos and bias in research and by wide human cultural variation (Dettwyler 1995). Also, the uniqueness of the human childhood phase has been critiqued by some who have noted in simians a similar slow growth and provisioning of juveniles by adults (Weisfeld 2006). However, they do admit within their critique that the food sharing to which they refer is generally with infants, not weaned young. Tanner described human growth curves as being a unique trait which is *shared* with other primates, distinguishing our order from other mammals (Tanner 1990).

Determining when the childhood phase developed in fossil *Homo* evolution, is something which paleoanthropology has focussed on predicting (Bogin & Smith 1996). Often based on estimations of life history variables in species such as *Homo erectus*. Before moving on to the history of those regressions, the next section will address the human juvenile phase and the second uniquely inserted human growth phase: adolescence.

### Section 2.3.1.C Human Juvenile Phase

Human children reach the juvenile phase from 5-7 yr, depending on which milestones are applied. The juvenile phase corresponds to the "middle childhood" phase in development psychology, with "early childhood" corresponding to the childhood phase, and "late childhood" starting with puberty/sexual maturity, i.e. adolescence (Thompson & Nelson 2011). By the age of 7, the first molars have reached functional occlusion, and full brain weight has been achieved (Bogin 1999b). Others designate an earlier age of ~5 yr for the beginning of the juvenile stage, based on reaching 90% of brain volume growth as a marker. The start of the juvenile stage is also marked by **adrenarche**.[17] Using adrenarche as the start of the juvenile stage would allow for better cross species comparison of this life history variable. The juvenile stage usually lasts until approximately age 10 for girls and 12 for boys, when the onset of puberty begins the adolescent growth phase. (Bogin 1999b).

### Section 2.3.1.D Human Adolescence

Like childhood, the insertion of the adolescent phase delays full sexual maturity, and allows for extended time for the full growth and development of the human brain. This extra time allows for the acquisition of skills—food provisioning & processing; parenting; technologies; social learning—as well as the acquisition of complex social identities. The adolescent phase starts with

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17. andrenarche: adrenal gland maturation stage which begins at about 7-8 yr, before the onset of puberty and continuing through puberty and adolescence. Adrenal androgen levels peak at around 20 yr and then gradually decline through life.

**gonadarche**[18]. The visible/physical signs of gonadarche are referred to as **puberty,** which starts at about 10 yr for girls and 12 yr for boys**.** Puberty involves the development of secondary sex characteristics. In the non-human African apes, gonadarche starts at approximately 7-11 yr (Thompson & Nelson 2011).

Adolescents contribute to the fertility of the group through alloparental care, and the adolescent phase represents additional time for acquiring and solidifying largely sex-defined suites of socioenvironmental survival skills (Bogin 1999b). The exact level of uniqueness of aspects of human adolescence are debated, with primatologists noting the presence of similar growth stages or patterns in large bodied, slow growing anthropoids.

After a childhood skeletal growth curve deficit, there is a significant, sexually dimorphic, adolescent **growth-spurt** (**GS**) observed at approximately 12 and 14 yr for girls and boys respectively—which allows humans to regain, temporarily surpass, and then rejoin chimpanzees growth curve levels (Smith & Tompkins 1995). At the peak of the adolescent GS, the average height velocity is +9cm/year for boys and +7.1/year for girls (Bogin 1999b). This skeletal growth spurt can be seen as another life history "catch-up" strategy which compensates for the energetic compromise of suppression of body growth rates until the completion of full brain size (Zollikofer *et al.* 2014).

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[18] gonadarche is the reinitiation of activity of the hypothalamic-pituitary-gonadal system of hormone production. GnRH production by the hypothalamus is inhibited after 2 years of age and gonadarche is triggered when a specific frequency and amplitude of secretion pulses is reached.

It should be noted that there is considerable debate about the level of uniqueness of human adolescent GS, as forms of GS are reported to exist in other primates (Weisfeld 2006). Some have defined the unique human growth spurt as being a skeletal growth spurt or "the rapid acceleration in the velocity of virtually all skeletal tissue" in humans (Bogin 1999b). However, other slow developing social primates also have periods of skeletal growth acceleration. As many primate studies haven't been able to use longitudinal data, the presence of growth rate spikes may have been missed because cross-sectional data will tend to smooth out, shorten, and flatten any growth rate spikes which could have been present (German & Stewart 2002).

Additionally, there are many reports of primate body weight growth spurts (GS) in various species. Also in exploring how LH variables, such as growth rate spikes, are best observed in living primates, the question of which markers are collected and measured may have an impact. Length changes measured physically from a living sample may not reflect growth changes as as opposed to changes garnered from skeletal samples. Hormonal measures may help pick up visually subtle or non-observable changes in non-human primates. For instance, very recent research into bonobos has revealed that rather than assuming presence/absence of GS in other primates, both appropriate scaling and hormone level monitoring can make adrenarche, puberty, and GS more visible in non-human primates (Berghänel *et al.* 2023). These researchers demonstrated both linear and weight GS in bonobos, and hopefully future research will provide better comparative scales by which we can see the similarities and differences in human growth rates and stages more clearly. Developing uniform standards of collection and reporting of growth rates and stages will hopefully permit a more accurate comparison of human growth which would clarify whether humans are using catch-up growth in a different manner or degree to other primates in the future. Without this, the studies attempting to do project the presence/absence of a "human" growth spurt onto fossil hominins are premature.

Additionally, the human skeletal growth is not uniform throughout the body, with different regions reaching peak rates at different ages: feet are followed closely by hands and then legs; then arm length, standing height, and trunk length (Bogin 1999b). Muscle GS in humans is relatively greater than length GS and continues after length GS has peaked in boys, meaning peak muscle mass is achieved some 4 yr after peak height velocity (Bogin 1999b). Some areas which do not demonstrate a GS in humans are: adipose tissue; lymphatic tissues; thymus; and the female pelvis (Bogin 1999b).

### Section 2.3.1.E Human Reproductive Senescence

The third derived life stage in humans is the post-reproductive life stage, signalled by the abrupt process of menopause at approximately 50 yr across all human populations (the beginning of the process of cessation of ovarian function). While some primates in captivity have been shown to have a gradual decline in ovarian production and some cessation of ovulation shortly before death, human menopause is unique in an abrupt cessation of production of reproductive function unrelated to ovarian (synonym for cell decay/ organ ageing) and prior to general levels of (word for ageing) of other body systems. This period of non-reproductive life is theorised to allow women (e.g. grandmothers) to contribute to the reproductive success of their children through knowledge, teaching, allocare and provisioning, and various hypotheses have addressed if it led to or resulted from the evolution of modern human morphology, and when, in the evolution of hominins, this stage evolved (i.e. Grandmother Hypothesis).

## Section 2.4 Fossil Hominin Life History

Estimates of the life histories variables and life history patterns in fossil hominin species can be made using fossil and archaeological evidence to estimate: weaning ages, interbirth intervals (**IBI**), neonatal altriciality, initiation of juvenile stages, age of sexual maturity, and the potential presence of growth spurts or of a post-reproductive phase in individual fossil hominin species or grades. This section will discuss what LHRVs have been determined or estimated for fossil hominins. It will present what LHRVs are known for fossil hominins, with a focus on *H. erectus* s. l., as well as the implied life history patterns of fossil hominins.

Although most life history variables (LHVs) cannot be seen directly as biological data, some aspects of fossil hominin life history can be reconstructed through the fossil record as well as the inferences made by the archaeological record. Life history traits can be seen to fall into three categories: traits that directly record the timing of life history events (LHVs); qualitative and quantitative information from the fossil record that provide information about ontogeny (LHRVs); primate skeletal variables that have been shown to influence or correlate with LHVs (also LHRVs) that are recorded in the fossil record (Skinner & Wood 2006). What LHVs and LHRVs and are visible in the fossil record? Age at weaning is one LHV that has historically been thought to be recorded in fossil (Skinner & Wood 2006). LHRVs from the fossil record include, deciduous dental attrition, estimated body mass, neonatal ECV (measured and predicted), ECV, and dental traits including crown and root formation times, tooth timing patterns, and tooth emergence ages (Skinner & Wood 2006).

Dental attrition in *G. gorilla* has been shown to be related to diet (either through CF or early weaning) rather than to enamel thickness, timing etc (Aiello *et al.* 1991). However, the use of dental attrition as a proxy for weaning age in fossil species, may be problematic because in hominids (including humans) dietary supplementation (CF), which can accelerate attrition, can pre-date weaning by a number of years (Skinner & Wood 2006), Smith *et al.*, 2013). Plastic traits like weaning age are less fixed than traits like dental development, gestation length, etc (Lee, 2012). While bone chemistry studies in pre-historical skeletal samples have detected the timing of the introduction of CF alongside nursing, but have not been able to pinpoint exact weaning age, potentially due to the gradual and extended shift from nursing to weaning known to occur in "traditional" human societies (Stuart-Macadam 1995). There is strong historical evidence for nursing to continue to 2-3 yr from a number of societies, as well as writing detailing the high mortality rates (99.6% in orphanages and 50% in family homes) in infants who were neither breastfed nor supplemented with mammal milk (i.e. dry-nursed) (Stuart-Macadam 1995).

By the early 00s, increased details of the developmental differences between humans and chimpanzees had led to a growing consensus that Australopithecines and early *Homo* were closer in dental development timing to apes than humans (Anemone 2002). At the same time, while it was noted that *H. erectus* has historically been ascribed an "intermediate" life history pattern between ape and humans—especially with regard to the lack of a human-like adolescent growth spurt—the need for systematically assessed ages for *H. erectus* crania and for the development of cranial/facial skeletal references for assessing linear growth rates was raised (Antón 2002a).

The histology-derived $M_1$Ages of 2 Miocene apes, which are outside extant monkey ranges, and which progressed over time from 2.3 yr (17 Mya) to 3.4 yr (10 Mya), led Kelley Kelley (2002) to suggest that there was already a grade-shift in place for the hominid LCA. That is, hominids tendency toward increased body and brain size, extended periods of growth including slower dental development. He asserted that while increased cognition would have been in a positive feedback loop with other life history changes, explanations for the selective pressures which led to the modern human life history pattern should be found in factors *outside* of this shared grade shift (e.g. factors which initially reduced juvenile and adult mortality rates compared to non-human hominids).

Plio-Pleistocene hominins (e.g.the Australopiths and early *Homo*) teeth were unique enough in both morphology and development that many authors have emphasised not ascribing ape- or human-like affinities to these taxa (Benyon & Dean 1988; Aiello & Dean 2002; Ramirez-Rozzi 2002). When researchers are able to establish more appropriate dental development standards specific to fossil hominins, age/stage results and conclusions differ from those applying either/or extant standard (Ramirez-Rozzi 2002). Note, this isn't assuming a "midway" point between the two for fossil hominins, as taxa have their own unique life history patterns. Care should be taken not to assume a linear trajectory between hominid life history and human life history, within which fossil hominins are assumed to fit. ECV regression can fail to fully describe the differences in $M_1$Age between closely related extant hominin species with differing tooth emergence schedules both because of issues with regression itself, but also because species variation is multifactorial in ways that ECV variation alone cannot reflect.

A recent study of the tooth development stage scores of mandible materials of *H. naledi* two immatures (one infant) found that deciduous dental development appeared more similar to humans than chimpanzees while permanent tooth emergence pattern was a mosaic of human-like and chimpanzee-like tooth development (Cofran & Walker 2017). While it should be noted that the deciduous formation pattern of the infant may be a function of it's age, a slower, more human-like, life history pattern would be unexpected for such a small brained hominin (Cofran & Walker 2017). Referring back to extant primates again, Pan and Pongo are very similar in ECV but different in life history pacing, and potentially very different in $M_1$Age. The high level of primate intra-specific variability of $M_1$Age is noted and caution is urged with regard to making conclusions based on dental correlations about fossil hominin growth stage extensions (Bermúdez de Castro *et al.* 2015).

### Section 2.4.1 Neonatal ECV

Studies using *P. troglodytes* and *H. sapiens* neonatal ECV to estimate *H. e. erectus* neonatal ECV suggest that fossil hominins did not have chimpanzee-like patterns of prenatal brain growth (DeSilva & Lesnik 2006). In a study using the Mojokerto infant cranium to estimate neonatal ECV for *H. erectus, H. erectus* has been predicted to have had brain growth rates falling within the lower end of the modern human range, indicating that an increase in energetic demands of hominin neonates may have evolved by at least 1 Mya (Cofran & DeSilva 2015). More recently, regressions of primate ECV and molar proportions have reconstructed prenatal growth rates for fossil hominins to predict a shift in fossil hominins to human-like prenatal growth rates after 1 Mya (Monson *et al.* 2022).

### Section 2.4.2 Body Mass/Stature

In mammals, body mass positively correlates with many life history variables, such as weaning age, gestation, IBI, life span, etc ((Harvey & Clutton-

Brock 1985; Skinner & Wood 2006). The problem with using body mass in regressions to predict life history variables in fossil species is that body mass itself is estimated in fossil hominins using proxies and regressions (Skinner & Wood 2006). Both post-cranial and cranial methods have been used to estimate fossil taxa body size, including: modern human hindlimb joint size; hominoid-derived orbital area or orbital height; femoral head diameter; stature and bi-iliac breadth; upper limb joint size (Skinner & Wood 2006). Based on sexual dimorphism ratios, body mass in fossil hominins has been calculated have been greater than or equal to *Pan troglodytes* up until early *Homo* or *H. erectus* s. l. (depending on use of splitting or lumping respectively), becoming slightly lower than chimpanzees from 2 Mya onwards (Skinner & Wood 2006).

### Section 2.4.3 Material culture evidence

In later *Homo erectus* s.l., the possibility of insertion of a childhood phase in their life history is supported by increases in tool complexity, adoption of technology (fire and shelter) which indicate the increased social organisation and complexity that would support the nutritional needs of offspring that possess a childhood phase of development (Bogin 1999a, b; Klein 2009). Is has been postulated that scavenging carcasses to acquire bone marrow may have been done to provision childhood stage foods (Potts 1988; Bogin 1999a). The rest of the fossil hominin life history discussion, focussing on fossil hominin $M_1$Age estimates, will be covered in Chapter 4. Before moving on to the data in Chapter

4, the history and definition of *H. erectus,* the species whose $M_1$Age data is being used as a "test point" in this study, will be presented next in Chapter 3.

# Chapter 3

# Chapter 3 *Homo erectus*: Backgrounds

From Dubois' initial discovery of the species initially dubbed "*Pithecanthropus erectus*" in the late 19th century, the debates on the definition and taxonomic divisions of the ***Homo erectus*** **sensu lato hypodigm** have shifted over time and remain unresolved to this day. The many species/sub-species names found in the literature can at times be conflicting and confusing. Therefore, it is important to define the species terms as used in this text and to provide and overview of the dichotomy of views in this debate. Much of the debate can still be divided into two main camps.

The first camp holds that the *Homo erectus* hypodigm represents a polymorphic/polytypic chrono-species which includes the African, Asian and possibly European fossils (e.g.Brauer & Mbua 1992; Walker & Leakey 1993). This view applies Mayr's criteria of species as a reproductively distinct lineage persisting over time and does not tend to apply phylogenetic significance to minor morphological variations (Suwa *et al.* 2007).

While the African populations are similar to the Asian populations, regional differences are seen. In this second camp, phylogenetic significance is assigned to these minor cranial dental variations to group the fossils into multiple hypodigms. These are largely Asian *Homo erectus* s.s. and African *Homo ergaster,* but with a number of early African fossils, such as OH 9 and OH 12 in African *H. erectus* (Suwa *et al.* 2007). Some place all of the African fossils into *H. ergaster* as a single lineage, restricting the use of *H. erectus* specifically to the

Asian fossils (e.g.Tattersall 2013). In this view, the *H. ergaster* clade is ancestral to *H. erectus* s.s. and to all later *Homo* species.

Often, the compromise term has been *H. erectus* s.l., but frequently there is a trend towards using *Homo erectus/ergaster* to refer to all of the fossils. Additionally, this is not the limit of the debate. For instance, there is division over whether *H. habilis* and *H. rudolfensis* belong to a single or separate species. Others propose the two should be placed within the genus *Australopithecus* (Wood 1999). The various camps with regard to the groupings and divisions of Middle and Late Pleistocene *Homo* species are also substantial.

It is not within the purview of this study to resolve the debate over the appropriate *H. erectus/ergaster* divide. However, my perspective on the taxonomy and definition of the hypodigm is contextually pertinent to the application of the regression equations produced and the discussion of prediction outputs (Chapters 4 and 5). Therefore, I will provide a concise definition of *H. erectus* near the end of this section.

Firstly, I will provide a brief overview of the the historical contexts of *H. erectus* fossil discoveries and past taxonomic philosophies. Secondly, I proceed with an overview of the contexts of the ongoing debate between "splitting" or "lumping" or doing something else with the hypodigm. Finally, I provide my working definition of the *Homo erectus* taxonomic definition that will be used throughout this thesis.

## Section 3.1 *Homo erectus*: Taxonomy History

Taxonomic boundaries are, by necessity, based on the available fossil materials at the time. As new discoveries are made, there is a tendency for these novel populations to possess new traits or previously unknown combinations of traits which can challenge established taxonomic boundaries. Because recovered fossil populations are relatively rare, and recovered populations/sites are widely dispersed through space and time, the traits used to define taxonomic boundaries are limited. Thus, each newly recovered fossil hominin presents palaeoanthropologists with a dilemma: assign the discovery to an existing palaeospecies; use it to define a new genus/species/subspecies/deme; adapt existing naming devices in new ways to fit new, unexpected features; or avoid assigning taxonomy in early analysis by using descriptive terms relative to existing groups (Dennell 2009).

Trends of taxonomic naming and boundary adjustment have varied over time, especially with regard to the *H. erectus* s.l. hypodigm. In this section I will provide a concise overview of the history of these trends. For simplicity's sake this will largely be delineated into four "ages": Splitting, Lumping, Dumping, and Mosaic. This will be followed by an attempt to summarise a degree of current discourse, although a lack of resolution and general consensus on the issue remains.

Some concepts dealt with in the next section may be briefly mentioned or introduced here, but further discussion of their impacts, support, or later rejection will be reserved for after the historical overview. The most important thing to note, before delving in, is that the debate over the hypodigm and phylogeny of *H. erectus/ergaster* is ongoing and can be divisive and it certainly will not be settled within the scope of this thesis. Nevertheless, the species' history provides important context.

### Section 3.1.1 Palaeoanthropological Infancy: "Splitting Age" (Darwinism & Novel Taxonomy)

In the late 19th century, driven by a research goal of recovering fossil evidence to support Darwin's theory of the existence of a species morphologically intermediate to extant apes and modern humans, Dr. Eugene Dubois travelled to the Indonesian island of Java. The first Neanderthal fossils were recovered approximately half a century prior, but Darwin's proposed "missing link" had not yet been found. Near Trinil, in 1891 Dubois recovered his first fossil hominin specimen, for which he initially created the genus *Anthropithecus*--later calling it *Pithecanthropus* (Dubois 1896; Groves 2001). Dubois emphasised the bipedality of this hominin--suggested by morphology of the "Trinil femur"--by labelling this hominin as *Pithecanthropus erectus*, which loosely translates to "upright ape man."

With little other available material for comparison, early researchers tended to create new **taxa** for each newly discovered locality (see Table 3.1). Thus, early palaeoanthropologists are sometimes described as having a tendency towards taxonomic "splitting." Within Indonesia, this is partly due to Dubois' staunch refusal to allow any fossils outside of Trinil/Sangiran to be classified as

*Pithecanthropus.* Occasionally the proliferation of names was a result of attempting to rename existing fossil populations, rather than a further proliferation of species.

It is also noted that not all researchers of this period believed that the use of novel taxa represented evidence for speciation. Species names, much like site based names for fossils (e.g. Trinil, Kabwe, etc) were placeholders. Weidenreich (1943)—who viewed human evolution as unilineal—viewed the use of novel taxa in palaeoanthropology as a tool for facilitating the identification of different fossil groups, not evidence of speciation, as such. Despite this, Weidenreich had, by 1940, identified that the many varied names were leading to misinterpretations of the relationships of the fossils. Weidenreich (1940) proposed that *Sinanthropus* and *Pithecanthropus* be considered two subspecies of a *Homo* species: *Homo erectus pekinensis* and *Homo erectus javanensis* and that the Ngandong hominins be re-classed from *H. soloensis* to *H. neanderthalensis soloensis.*

### Section 3.1.2 BSC & Post-war synonymisation: "Lumping Age"

Despite Weidenreich's 1940 proposal, this tendency to assign novel taxa to new fossil localities remained prevalent for some time. As Weidenreich's sub-specification shows, this era—from the 1900s through WW2—was not a period during which there was any lack of discussion of the issues with the proliferation of taxa. An early proponent of rationalisation was Theodosius Dobzhansky who followed on from Weidenreich's work but did not share the opinion that species

**TABLE 3.1 *HOMO ERECTUS* 'NAMES', PRE-SYNONYMISATION**

| Year | Genus | By |
|---|---|---|
| 1892 | *Anthropithecus* | Dubois |
| 1894 | *Pithecanthropus* | Dubois |
| 1900 | *Proanthropus* | Wisler |
| 1927 | *Sinanthropus* | Black |
| 1932 | *Javanthropus* | Oppenoorth |
| 1932 | *Praehomo* | Oppenoorth |
| 1938 | *Africanthropus* | Weinart |
| 1940 | *Meganthropus* | Weidenreich |
| 1950 | *Telanthropus* | Broom & Robinson |
| 1954 | *Atlanthropus* | Arambourg |
| 1965 | *Tchadanthropus* | Coppens |

Compiled from Groves (2001; 2009).

were just helpful categories. Applying biological species concepts, Dobzhansky (1944) proposed that *Sinanthropus* and *Pithecanthropus* were not dissimilar enough to represent separate species, but were two closely related "races"[19] of the same species: *Homo erectus*. It is worth noting that his ideas are commonly attributed to Ernst Mayr. Mayr (1944) proposed sinking the Chinese *Sinanthropus* fossils into Javan species *Pithecanthropus erectus*. Mayr demonstrated that the **generics** being used for hominids had no biological significance in systematic zoology (Mayr 1950; Antón 2003; Tattersall 2013). This idea later led authors such as Campbell and Howell to regroup the various taxa (see Table 3.1) into the genus *Homo* as the species *Homo erectus* (Zeitoun 2009). This included fossils from Africa *as well as* Asia. This wasn't widely adopted until after the 1962 Symposium of Wartenstein was widely championed

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[19] defined as "populations differing in the incidence of certain genes, but actually exchanging or potentially able to exchange genes across whatever boundaries (usually geographic) separate them" (Dobzhansky 1944:252)

widely by Campbell from 1963 onwards (Zeitoun 2009). Though, this placement of the hominins intermediate to *H. neanderthalensis* and the Australopiths within the genus *Homo* took some time—demonstrated by the creation of *Tchadanthropus uxoris* (Coppens 1966) and by the continued use of *Atlanthropus* (Ennouchi 1975).

During this period, following synomisation, *Homo erectus* was generally presumed to be the only intermediate after the Australopithecines or *Homo habilis*, and the ancestor to all subsequent *Homo* species (Antón 2003; Zeitoun 2009). There was a general avoidance of the species proliferation of early paleoanthropology. Rather than assign new specifics, many potentially transitional European Middle Pleistocene hominin fossils (no longer currently considered to fall within the *H. erectus* s.l. hypodigm) were either treated as late examples *H. erectus,* or referred to by the use of grade classifications, or with the term "archaic *Homo sapiens*" (Dennell 2009).

Additionally, due to a lack of post-Australopith materials recovered from Africa until the 1960s, *Pithecanthropus/Sinanthropus* had been believed to be limited to the Eurasian continent. This view of *H. erectus* as an Asian species changed with the recovery of mandibles at Ternifine, Algeria, (e.g. *Atlanthropus*) followed shortly after by the recovery of hominin material at Olduvai, Tanzania (le Gross Clark 1964, 1964). *H. erectus* criteria was also generally defined as being limited to fossil populations whose crania shared a "heaviness" of morphology and an average ECV above ~ 1000 ml (Howells 1980).

This period of lumping the middle ground specimens (between *H. habilis* and *H. sapiens* subspecies) into *H. erectus* s.l. gave way to a new era of thought on hominin taxonomy. Proliferation of African fossil discoveries, along with advances in modern human mt-DNA research (which indicates a recent African origin for *H. sapiens*) led the conclusion that perhaps the *H. erectus* net was cast too wide. A new species, *H. ergaster*, relegated the Asian fossils (*H. erectus s. s.*) to a dead-end side branch in the human lineage. This split between *H. ergaster* and *H. erectus* s.s. became key to the debate between Replacement Theorists and Multi-Regional Evolutionists. Before presenting this shift, however, the history of Movius' line (1948), it's continued impact within the *H. ergaster/ erectus* splitting debates, and it's lack of scientific validity will be discussed.

### Section 3.1.3 Movius' so-called Line

Following on from their 1937 fieldwork in Burma, Hallam Movius, Helmut de Terra, and Teilhard de Chardin, were joined on an fieldwork season in Java, Indonesia, by G.H.R. von Koenigswald in the summer of 1938 (Dennell 2014). The ideas they discussed during these field seasons led to the development of the young Hallam Movius' (1948) publication of a theory now generally referred to as the Movius Line Theory (hereafter MVT). Movius held that a region containing East and South East Asia (i.e. everything East of his imaginary boundary line) retained a more primitive form of lithic technology into the Late Pleistocene or Early Holocene (Dennell 2014). In contrast to the more "advanced" "Hand-Axe Culture" of the west, this region (defined by an imaginary line separating the areas North and East of Africa, India, SW Asia, and Europe) was represented on his map by small, seemingly isolated, areas of "Lower Palaeolithic Chopping-Tool Cultures" (Movius 1948).

Movius viewed this East/West Line as definitive of both behavioural and biological differences in the Eastern hominins (Lycett & Bae 2010). This belief in the primitive nature of the "remote" Asian hominins and their "culturally retarded" tool complexes--in contrast to the perceived dynamic and evolved nature of Western European hominins—was clearly influenced by the cultural biases of his time (Dennell 2014).

The lack of a uniformly patterned complex of bifacial hand axes appears to frequently translate into a complete lack of stone tool creation anywhere in East/ Southeast Asia and the frequent exploration of what biodegradable tools were being used instead of stone tools behind the "Movius Line." However, this practice requires forgetting that there are East Asian hominin sites with extensive stone tool assemblages. At Zhoukoudian, some 17000 flaked stone artefacts have been recovered from across the 27 occupation levels (Dennell 2009).

In fact, an early misrepresentation of the lithics at Zhoukoudian contributed to MVT. A visit to Zhoukoudian by Teilhard de Chardin and Pei (1932, as cited in Shen *et al.* 2016) mischaracterised of the assemblage as a handful of crude tools which represented a "Chopper-Chopping Tool Industry": an idea which became embedded in MVT (Shen *et al.* 2016). In contrast to the original assessment of this assemblage, recent preliminary use-wear analysis of the Late Phase levels of the cave indicate morphologically typed created for specific uses, as well as variability of use of common tools (e.g. scrapers) in different periods or localities of the site (Shen *et al.* 2016). It has also been noted that discourses of European Middle Paleolithic assemblages similarly lacking in bifaces have tended to apply ecological explanations or variations in local cultural traditions rather than relying on explanations which imply "primitive" levels of development (Dennell 2016).

Despite more recent evidence of "hand-axes" and other lithic technologies in East Asia and of the inaccuracies of the original publication that originated it, the MVT has not been abandoned in favour of a theory which is supported by the data. Instead there continues to be a tendency within the field to attempt to modify the theory in order to validate it for continued use (e.g. Lycett & Bae

2010). Indeed, the MVT is referenced as Movius' "insightful observation" in recently published texts (Wang *et al.* 2023). This same text also applies the term "chopper-chopping tool industry"—to describe the Bose Basin area earliest stone tool assemblage. This repeats the inaccurate terminology once applied by Movius to the Zhoukoudian tools which are now known to be chert cores which were used in the production of flake tools (Shen *et al.* 2016). The shifting definition of an Acheulean assemblage has not always been applied equally to Asian lithics. Asian sites with a low percentage of total bifaces—which may simply reflect a smaller assemblage size—are excluded from classification as Acheulean, while, on the other hand, a redefinition of the Acheulean has been proposed which would include specific African sites which do not contain *any* bifaces (Dennell 2018). The assertion that the MVT is biased, scientifically unfounded, and impedes discourse on hominin settlement within East and South East Asia appears to be valid (Dennell 2014, 2016). It is therefore noted that the ongoing, and often uncritical, use of the MVT illustrates where *some* of the assumptions of Replacement Theory in relation to the evidence supporting it (e.g. migration before the evolution of the Acheulean used to imply of evolutionary "stagnancy" or primitive levels of cognition in Asian *H. erectus s.s.*) and in turn the assumptions associated with the creation of the species *Homo ergaster*, may derive from biased foundations. The next subsection will review the renewed tendency—in the final quarter of the 20th century—for the creation of novel specifics for early and later *Homo* species fossils.

### Section 3.1.4 "African Eve", Novel specifics & "Dumping" Asian *H. erectus*

Into the latter quarter of the 20th century, continuing fossil discoveries in Africa—along with new human **MT-DNA** research—indicated the possible existence of one or more pre-erectus *Homo* taxa and *Homo erectus* sub-species, as well as a speciation of the human lineage within Africa at approximately 200 kya (Lahr & Foley 1998; Antón 2003). Much needed taxonomic sorting and analysis led to a focus on hominin **divergence** and **replacement**, and a renewed interest in taxonomic diversification, the tendency swung back towards a the use of diverse array of new and revived **taxa** and **specifics** (Dennell 2009). Previously abandoned **specifics**, such as *Homo heidelbergensis* and *Homo helmei* were now suggested for morphologically unique larger brained, transitional European Middle Pleistocene hominins (Lahr & Foley 1998). Additionally many of the small-brained fossil hominins which had originally been placed in the *H. erectus* s.l. hypodigm are now widely accepted to fall into their own species (i.e. *Homo habilis* and/or *Homo rudolphensis*).

At the time the limited fossil *Homo* species sites and the lack of known Acheulean assemblage sites outside of Africa pre-dating 1 Mya, were taken as support for the assumptions of the Movius Line. The Asian *Homo erectus* lineage *must* have left Africa shortly before an assumed speciation event that led to the behavioural changes demonstrated by the Acheulean assemblages in Africa.

To explain the perceived lack of behavioural advances in Asian *H. erectus* and the morphological variations in new fossil materials being recovered, Groves and Mazák (1975, cited in Wood & Boyle 2016) proposed a new specific for the KNM-ER 1992 mandible from Kenya: *Homo ergaster.* Although their proposal was initially dismissed, due to the limited fossil material it was based on, the specific eventually began to be widely adopted for most of the Early Pleistocene African materials (see Klein 2009).

African *Homo ergaster* became viewed as the ancestor to all subsequent *Homo* species including Asian *Homo erectus* s.s. (which was relegated to an evolutionary side branch). Proponents of a speciation event within early African *Homo*, would embrace a Plio-Pleistocene *H. erectus* dispersal into Asia, because it fit the idea that Asian *H. erectus* left before the emergence of more complex forms in Africa, and reinforced Asian *H. erectus'* position as an evolutionary side-branch (Etler 1996).

Some East Asian researchers have viewed regional Middle and Late Pleistocene transitional *Homo* fossils to have a lineage which includes E. Asian *H. erectus*. Others have linked earlier and later *Homo* fossils within the Indonesian sites. Dennell (2004) has noted that fossil populations with temporal gaps can also be explained by population migration *out of* during periods when that local environment becomes inhospitable. In other words, absence *during* a time period does not necessarily represent an extinction event for the species. Additionally, subsequent presence within a site or region does not automatically indicate a *direct* ancestral relationshi*p.* Similarly, subsequent presence of morphologically dissimilar populations doesn't necessarily represent a "replacement" event when there is no direct evidence of temporal overlap. Given updated dating analysis of some Indonesian populations, is now thought to be more likely, for instance, that *H. erectus*(or *H. soloensis*) was "locally extinct" in Southeast Asia before the arrival of *H. sapiens* (Dennell, 2014).

While the dichotomy between the theories of Polytypic *H. erectus* s.l and a *Homo ergaster/erectus* lineage split would *seem* to follow the similarly dichotomous Replacement vs. Multi-regional debate, there is nothing within the theory of Polytypic *H. erectus* that would suggest that it is not parsimonious with mt-DNA research, African Eve, or Replacement theory. In other words, neither the a lack of a Plio-Pleistocene speciation event, nor a wider morphological/ geographical definition for *H. erectus* s.l., is in opposition to the African origin of *H. sapiens*. However, the widespread support for an Early Pleistocene *H. ergaster/African H. erectus* speciation event as key to the African Eve theory, has meant that some evidence non-parsimonious with this split has been rejected outright or has been slow to be accepted (e.g. Shipman 2000). One example of this is the case of delayed acceptance of the age and significance the Dmanisi Mandible, presented in 1991, which will be discussed in the next section.

### Section 3.1.5 Millenial Mosaics: Dmanisi, Dispersal, and Beyond

In the early 1990s, the debate between Multi-regionalists and Replacement theorists not withstanding, it was generally widely understood that *Homo* species had not existed outside of Africa before ~1.0 Mya. While there were a not-insignificant number of researchers reporting earlier ages at East and Southeast Asian site, these ages were not readily accepted. For example, the reported age of 1.9 Mya for the Mojokerto infant was rejected in favour of Middle or Late Pleistocene age, and a reported age of 1.2 Mya had been rejected in favour of 0.83 Mya (Pope 1988). At other Java Island sites with earlier geological ages, up to 1.9 Mya, the fossil materials from these levels were still considered to belong a species of a proposed australopithecine: *Meganthropus* (Jacob & Curtiss 1971). These specimens have since been demonstrated to be part of the *Homo erectus* hypodigm--consistent with Dubois' original assessment of the teeth (Smith *et al.* 2009). While provenance and stratigraphy of some of Asian materials has historically been an issue, more recent recovery of *Homo erectus* fossils in situ from securely stratified excavations have returned ages up to 1.5 Mya (Zaim *et al.* 2011).

However, the lack of pre-1.0 Mya antiquity for Asian *H. erectus* was widely accepted when the first hominid material recovered from SW Eurasia--the 1.78 Mya Dmanisi *H. erectus* mandible--was presented at the 1991 Senckenberg Institute colloquium in Frankfurt. Although the Dmanisi mandible is reported to have been immediately visually recognised by Walker as so similar to the mandible of the KNM-WT 15000 juvenile he dubbed them 'twins', their discovery was largely overshadowed at the conference by the Single *Homo* Species debate started by Wood and colleagues (Shipman 2000). At this same conference, a team of Japanese and Indonesian researchers presented their geochronology of Sangiran dome sites, which suggested that *Homo erectus* occupation in Java may have occurred as early as 1.4 Mya (Itihara *et al.* 1994).

Subsequently, new finds revealed the first occurrence of Acheulean assemblages happened as early as 1.4 Mya. Additionally, late-persisting 0.78 Mya European Oldowan assemblages were challenging the notion of unilateral evolution of stone tool technologies necessarily occurring simultaneously with morphological changes (Shipman 2000). Evidence was published that suggested hominin occupation of the Trinil locality, Java, as early as 1.8 Mya (Swisher *et al.* 1994). If these dates are taken as correct, this would mean that *Homo erectus* in Java slightly predated the earliest known African *H. erectus* s.s. specimen (KNM-ER 3733 at 1.77 Mya). However, this date still supports the theory that Asian populations dispersed from Africa before the earliest known date of Acheulean assemblages (1.4 Mya). Additionally, data showed that *H. erectus* (as *H. e. soloensis* or *H. soloensis*) persistence in Southeast Asia appeared to extend far into the Late Pleistocene, as demonstrated by ESR and U-series derived dates as late as 0.06 Mya at Ngandong and Sambungmacan sites in Central Java (Swisher *et al.* 1996). Newly published data from China suggested that hominin occupation of East Asia could have happened as early as 1.9 Mya (Shipman 2000). It should be noted that even much less ancient dates, such as the 1.6 to

1.1 Mya dates for Nihewan Basin localities in China are rejected by some researchers (Klein 2009).

At Dmanisi, nearly 10 yr after their initial mandible find, Gabunia *et al.* (2000) go on to discover two *H. erectus* skulls (D2280 and D2282), in situ with approximately 1000 Oldowan stone tools, dated 1.78 Mya. By that time the scientific community had began to experience a 'paradigm shift' in thinking about *Homo erectus* migration out of Africa prior to 1.0 Mya, and there would be widespread acceptance of the Dmanisi material (Shipman 2000). However, it should be noted that Schwartz (2000) was less ready at that time to accept these Dmanisi specimens as part of the *H. ergaster/erectus* hypodigm, preferring instead to suggest that the multiple specimens recovered from this this chronologically discrete hominin occupation actually represented multiple new hominin species. Indeed, nearly 10 years after this discovery, despite the intermediately mosaic *H. habilis/H. erectus* features and "primitively" smaller ECV of the Dmanisi hominins--that would appear to support an earlier geochronology for these hominins--Klein's (2009) textbook was teaching that the Dmanisi hominins are instead only ~1.0 Mya old, and formed part of a late persisting *Homo ergaster* clade (along with the Buia and Daka hominins)..

Comparative energetics research was demonstrating that "high-protein packages"--required to supply the greater energy requirements of a larger hominin body and brain--was likely a more important driver of hominin **dispersal** than any proposed benefit of acquiring an Acheulean tool kit (Antón *et* *al.* 2001). This conclusion is parsimonious with the earliest occupations Southwest (Dmanisi) and Southeast (Sangiran Dome) Asia occurring almost immediately after the first appearance of *Homo erectus* s.l. and a few hundred thousand years prior to the first occurrence of the Acheulean tradition. The relative body size increase of *H. erectus* would also predict for a 10-fold increase in home range size compared with that of Australopithecines. Coming into the 21st century, new evidence began to shift the prevailing views of hominin dispersal into Eurasia.

Thinking back to Howell's (1980) minimum features of a *H. erectus* population: similar in feature to descriptions of Asian *H. erectus*, especially with regard to cranial "heaviness", and having an average ECV of at least 1000ml. While most definitions do entail more nuanced than that, given the generalist understanding of the species, it may be unsurprising that first few decades of the 21st century have involved a lot of "surprising" and "unexpected" fossil discoveries of specimens described as having a "mosaic" of "primitive" and "advanced" traits. Additionally, since the discovery of KNM-WT 15000 skeleton, the extent of traits shared with *H. sapiens* had been emphasised, meaning discoveries of smaller specimens..

Moving forward into the 00s, reports of "mosaic" specimens of *H. erectus* or "erectus-like" fossils, in addition to Dmanisi, which challenge the idea of the known limits of *H. erectus* temporal, geographical, and morphological features.

This led many authors to describe the finds as "surprising" examples of erectus-like fossils in the wrong place, the wrong time, or of the wrong size.

As early as 1985, the Moroccan fossils from Thomas Quarry and Sale, are noted to display mosaic *H. erectus* and *H. sapiens* traits (Hublin 1985). Then in 1998, a newly recovered hominin, UA 31, from a 1 Mya early-Middle Pleistocene site in Eritrea, had an estimated ECV of ~750-800 ml, and is described as having a "mosaic of primitive and progressive features", indicating a transition towards human-like features ~0.3 Mya earlier than previously estimated (Abbate *et al.* 1998). Skulls start to be uncovered at the Dmanisi mandible site in 2001, with additional materials recovered in subsequent years, although some won't be published until 2013 (Lordkipanidze *et al.* 2013a). Histological techniques reveal *H. erectus* dental timing has shifted further from an "ape-like" pattern than the Australopiths, but that a "human-like" pattern had not yet evolved in *H. erectus*: S7-37 (East Asian *H. erectus* M1) histologically calculated $M_1$Age = 4.4 yr; KNM-WT 15000 estimated $M_1$Age = 4.0 yr (Dean *et al.* 2001).

A contemporaneous *H. erectus* calvaria, Bou-VP-2/66, or "Daka calvaria" is then described from the 1 Mya Dakanihylo Member of the Bouri Formation, Middle Awash, Ethiopia, a layer yielding an abundance of early Acheulean stone tools; ECV ~ 995ml (Asfaw *et al.* 2002). Daka can not be distinguished from either the Asian or African *H. erectus* fossils and, further is seen as evidence that hypotheses that the *H. ergaster* hypodigm may contain multiple species is unsupported by the data. Daka is seen to demonstrate that, while later populations in Asia ~ 0.5 Mya are differentiated from African *Homo* species, but prior to that, ~1 Mya, hominins of ~1000 ml are distributed throughout the Old World (Gilbert *et al.* 2003). Further analysis of UA 31 also measured ECV at 995ml (Macchiarelli *et al.* 2004).

At a similar time, the re-evaluation of crania from Broken Hill, Elandsfontein, and Bodo in Africa, and Arago and Petralona in Europe prompt the description of a new Middle Pleistocene species under the (revived) name of *Homo heidelbergensis* (Rightmire 2001). At a 0.97 Mya Acheulean site from Olorgesailie, Kenya, the KNM-OL 45500 partial cranium is described with an estimated ECV < 800ml and appears to share traits with African *H. erectus, H. e. georgicus,* and *H. ergaster/*African *H. heidelbergensis,* demonstrating the mosaic nature of the hominins from the period (Potts *et al.* 2004; Spoor *et al.* 2007).

In 2005, at the Dmanisi site, the skull of the oldest known (1.8 Mya) toothless hominin is described (Lordkipanidze *et al.* 2005). In 2007, 8 craniodental fossils at the ~1.4 Mya site at Konso, Ethiopia, described as having a mosaic of features more primitive than other *H. erectus* in combination with derived *H. erectus* features (Suwa *et al.* 2007). This pushes back the earliest date of Acheulean complexes. This challenges the assumption that tool making cultural adaptations are biologically mediated (i.e. the result of a speciation event) and the idea that the presence of a tool complex is necessarily linked to the absence of primitive morphological traits.

The post-cranial materials from Dmanisi are described in 2007 (Lordkipanidze *et al.* 2007). The Gona pelvis is published in 2008, which was evidence of early, 1.8 Mya, recognisable pelvic dimorphism despite the individual's small stature. The dimensions of the pelvis challenge earlier calculations of a lack of pelvic expansion for larger brained neonates in *H. erectus* drawn from the sub-adult male KNM-WT 15000 pelvis as well as estimated neonatal ECV limits of ~230ml for *H. erectus* (Simpson *et al.* 2008).

These discoveries challenge previous expectations of the ranges and levels of variability for *H. erectus* ECV, stature and development patterns and begin provide a more detailed picture of a hominin species with a body plan and behaviour set which is not fully modern nor fully primitive (Antón 2013). Over the course of this time period the first human genome sequence is completed in 2003 (NHGRI). The Neanderthal nuclear genome sequence is published in 2010 (Green *et al.* 2010) and that same year a partial sequence of the Denisova Cave, Siberia hominin finger mt-DNA is published (Reich *et al.* 2010). Paleogenomics has begun to have an increasing impact on palaeoanthropological discourse.[20]

While it is a bit harder to quantify where the debate over the position and extent of *H. erectus* hypodigm is landing or travelling at this time, it is clear that energetics & genetics research, dental histology, the expansion of fossil record, and the proliferation of "mosaic" specimens (both within *H. erectus* and other *Homo* species) have impacted estimations of the species. The impact of

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[20] Incidentally this impact in human biology and paleobiology is so great that the founder of the discipline, Svante Pääbo will go on to receive the Nobel Prize in Physiology/Medicine in 2022 (Nobelfösamlingen 2022)

paleogenomics, alongside the expanding record for *H. sapiens* and other *Homo* species sites throughout Africa and Eurasia has also led to some reevaluations of *H. sapiens* definitions and evolutionary theories.

Recently, a group of over 20 palaeoanthropologists challenged the view that humans evolved within a single population or single region of Africa: the Structured African Metapopulation Model (Scerri *et al.* 2018). They propose viewing the *H. sapiens* clade as an evolving lineage with deep population structure rooted in Africa. The clade evolved from highly diversified and subdivided populations living across Africa and connected by sporadic gene flow (including back-migrations and possible hybridisations with more divergent hominins living in different regions). Within this view, they believe it is possible that *H. sapiens* evolved from the more "primitive" *H. erectus* or *H. antecessor* rather than from *H. heidelbergensis*. Diagnostics of the clade should "reflect trajectories of evolution" rather than static states at points in time (Scerri *et al.* 2019). In a further clarification of this critique of the "simple out-of-Africa" model (**SOA**), Scerri *et al.* (2018) emphasise that humans did not *leave* Africa, humans *expanded* our range, like many other mammalian species and hominins before us. This is neither a traditional Multi-Regional model nor a Replacement model..

Where does this leave *H. erectus*? The position on this with regard to *H. erectus* seems to be one of continued polytypic similarities across populations throughout an expanded range for some time, until divergences of the African *Homo* fossils from the Asian fossil become obvious from 0.5 Mya onwards. Many seem to find a lack of evidence for a speciation event in early *H. erectus/ ergaster.* Part of the struggle in resolving the *H. ergaster* question may be that the original paratype provided no comparison with the Asian fossil record and a portion of it is no longer included in most *H. ergaster* hypodigms and the original description (Antón 2003).

## Section 3.2 *Homo erectus*: Definition

Until there is more substantial evidence for a speciation within early *Homo erectus s.l.,* the fossils should be treated as a single hypodigm. I follows Antón (2003) in viewing the hypodigm as "geographically replacing **allotaxa**". In populations which are morphologically diagnosable but not reproductively isolated, allotaxa solves the dichotomy where the phylogenetic species concept sees species and the biological species concept sees subspecies (Jolly 2001). That is, *Homo erectus* can be seen as a number of geographically and/or temporally separated **parapatric**[21] groups. In this manner, the ongoing, unresolvable debate is no longer the focus..

Why accept that the issue is unresolvable? Many attempts at reconstructing the hominin clade act as if the current fossil record is an accurate, detailed, and comprehensive reflection of the history of human evolution: it should be treated as incomplete and interpretation should be viewed as *heuristic devices* (Wood &

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[21] **parapatry** describes closely related populations which do not occur together except in narrow contact zones; this is in contrast to **sympatry** where closely related populations occupy the same zone without interbreeding

Smith 2022). Treating *H. erectus* and closely related specimens as a polymorphic allotaxa aids in analysis without necessarily assuming evolutionary lineages..

There is ample evidence that the traits traditionally used to differentiate *Homo erectus* sensu stricto from *Homo ergaster* are continuous variables rather than binary variables which only exhibit present or absent status (Brauer & Mbua 1992). Additionally, there are close affinities between the Asian and African specimens (Antón 2002b; Liu *et al.* 2005; Cartmill 2009). The evidence seems to lean towards the inclusion of *H. ergaster* within *H. erectus.* However, I have treated *H. e. ergaster* as a separate subspecific group in the later predictions so that potential outlier groups are visualised in contrast to the performance of the larger grou*p.* I label the *H. ergaster* fossils as a subspecies of *H. erectus*: *H. e. ergaster*. The position of the Dmanisi materials is somewhat less certain, given the interesting mosaic of primitive traits variably displayed within the grou*p.* Nonetheless, they share sufficient *H. erectus* similarities to warrant treating them as another subspecies: *H. e. georgicus*..

It may be premature to reconstruct life histories for specimens that may ultimately be found in future to represent distinct species (Antón 2002b). Therefore, I present the African and Asian populations as a group and as three regional sub-groups (e.g. African, East Asian, Southeast Asian) in analysing predictions..

On the matter of the Ngandong fossils: due to their very late age (with some estimates as late as 0.03-0.01 Mya) and the temporal gap from “classic”

Indonesian *H. erectus,* I follow Widianto & Zeitoun (2003) in treating them as *H. soloensis* and grouped them with the other Middle Pleistocene *Homo* species. The dating of the Sambungmacan and Ngawi fossils is a little less clear, as is the lineage of *Homo floresiensis* and I have not included them for analyses at this time. *Homo neanderthalensis* and fossil *H. sapiens* are treated as separate species and grouped together in the Late Pleistocene *Homo* species group..

Throughout this text[22] *H. erectus* or *H. e. erectus* will refer to all of the combined Asian and African *H. erectus* fossil populations*,* excluding any subspecies*,* unless otherwise noted. When *H. erectus* s.l. (or *H. erectus/ergaster*) is mentioned, this will include *H. e. ergaster.*

Regional variation will be taken into account as it affects life-history reconstruction. It is important to note that while the path to the evolution of the modern human life history pattern is of interest in relation to the reconstruction of hominin life histories, hominin life histories are themselves of interest in their own right. I will be focussing the background discussion on morphological traits that are used in reconstructions of ECV, body size, sexual dimorphism and daily energy requirements, all of which pertain to the reconstruction of *Homo erectus* life histories.

So why does *H. e. erectus* make a good test point? Firstly, there is an available $M_1$Age to test. Secondly, the degree of ECV variation within the hypodigm and the variable ways that hypodigm is split/grouped offer another

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[22] That is, when speaking specifically about the fossils. When discussing issues pertaining to the full hypodigm of *H. erectus* s.l. more generally, "*H. erectus*" will generally be inclusive of the proposed subspecies.

view from which to interpret regression predicted $M_1$Age. Mean ECV for sub-populations can be different enough to result in very different predicted $M_1$Age. Some of fossils which are frequently excluded from *H. erectus* in favour of other taxonomies, would have little impact on the larger species (s.l.) whether included or excluded, whereas others can skew ECV and therefor $M_1$Age prediction when included in the "s.l." Some parts of the *H. erectus* hypodigm overlap metrically in ECV range with Middle and Late Pleistocene *Homo* for ECV. Does all of the spatio-temporal-morphological variation equate to $M_1$Age and life history variance? How do we differentiate which ECV variation difference is directly tied to $M_1$Age difference and which overlap in ECV is not (e.g. *H. sapiens* and *H. neanderthalensis* which overlap for ECV range but appear to have variation in $M_1$Age). In the Australopiths, there appears to be very little total variation in $M_1$Age, despite speciation, and if regression $M_1$Age is applied to a polytypic species like *H. erectus* s.l., looking at just the mean of ECV age for the hypodigm would tend to obscure potential variation seen in sub-group populations from the extremes of *H. erectus* s.l. ECV variation (as will be visibly obvious in the figures of Chapter 6). The history of *H. erectus* s.l. offers examples of where a population(s) of fossils can be recovered and treated as representative of a hypodigm for which it is later shown to only represent a small amount of the total variation. Where ECV variation expands around a relatively stable mean, and therefore brain size is varying more extensively than the variation implied by regression predicted $M_1$Age (derived from the mean ECV), should this be interpreted as inertia in life history patterns? As an inaccuracy in the regression model? As a problem with the taxonomy? Is $M_1$Age regression better able to define $M_1$Age from ECV in more tightly defined species fossil hominin species?

# Chapter 4

# Chapter 4 Data & Regression Methods

This chapter explains how I have collated published primate data for this study, the regression methods employed to answer the questions of this thesis. To guide the structure of this and further chapters, the primary questions being asked will be reviewed. Then the chapter will be presented in two stages: data and methods.

The first question approached is: can the size of the primate paired $M_1$Age and ECV data set be increased (e.g. what has been published since the mid-1990s) and what impact would any increase have on the accuracy of predictions? Does the strong correlation still hold? This will include exploring whether fossil species, through the use of histologically derived $M_1$Ages, can be added to the data set, and what impact including them has on the accuracy of predictions. This will be addressed in the first section of this chapter.

The next question to be explored: do progressive taxonomic exclusions significantly change the performance of the predictions? As past regressions have seen improvement by excluding strepsirrhines from the data set, reducing the taxonomic levels included could further improve the correlation. It could also reduce the data set to the extent that the assumptions of the models being applied are failed. Also to be addressed is: does using a different type of regression equation change the performance of the data set? Ultimately, all these questions aim to answer the primary question: can regressions of $M_1$Age by ECV accurately predict (and by extension, early life history patterns) of *Homo* species (with a focus on *H. erectus* as a “test” case)? Most importantly, can they do so without post regression adjustments that rely on assumptions of “chimpanzee-like” or “human-like” patterns in the fossil species being predicted? The second section of this chapter will discuss how these questions are approached though regressions (with the results of the approach being later presented in Chapters 5 and 6, and the implications of those results further discussed in Chapter 7).

## Section 4.1 Data

This section now discusses what published primate $M_1$Age and matching ECV means I was able to access and compile for this study. It will present issues encountered with the available published data and why those issues exist. There will be some discussion of the minimum requirements introduced for the inclusion of a species as a datapoint, with a focus on attempts to increase the number of Hominoidea (especially the extant African apes) and what issues are encountered. I also consider the debate on “wild effect” with regard to the mean chimpanzee $M_1$Age.

This would be a good point to revisit the general issues with the published extant Primate data. As noted in the the more detailed discussion of primate life histories in Chapter 2 (Primate Life History), there are many issues with the availability and compatibility of published data across many life history variables. Therefore, before this chapter goes into the details of $M_1$Age and ECV data individually, I will touch on some highlights of issues with primate data collection and reporting.

### Section 4.1.1 Reporting and Sampling Issues

There are numerous data issues that have been noted within seminal primate life history texts (e.g. (e.g.Harvey & Clutton-Brock 1985; Harvey *et al.* 1987) on which many primate regression studies have historically relied on a portion of their species datas points for. These issues include unreferenced data, inappropriately applied genus estimates used for species, duplicated data points, applying inadequate data where more in-depth data may have been available, etc (seeSmith & Jungers 1997).

It is worth noting again that primate studies are not evenly sampled across the order due to sampling effort errors[23] in primate studies, and it is generally accepted that the distribution of observation efforts is understandably unequal (Hawes *et al.* 2013). This refers to how the impact of factors such as human access to primate environments, how observable the primates or the variable intervals are (physically, behaviourally, or temporally), and the various practicalities that impact study design (funding, length of time researchers are available, seasons researchers are available, study aims/research structures, etc) on how, where, and which wild primate data is recorded and reported. Species favoured for a larger number of captive populations (e.g. charismatic species or species historically favoured for laboratory testing) tend to have more recorded data.

Field study sample sizes tend to still be smaller than those in for captive primate studies (e.g. 5 wild versus 56 captive individuals in Smith *et al.* 2013). Access to skeletal data from deceased *extant* primate species, especially in those most closely related to us, is understandably also mediated by additional ethical considerations, especially where staff have had close interactions with the animals before they died. The appropriateness of each deceased juvenile individual as a reference point will also be effected by the manner of their death,

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23. sampling effort errors occur due to the nature of primate environments, distribution, and many unavoidable practical considerations and the term should not be taken to reflect any neglect or lack of diligence on the part of primate researchers

as it has been highlighted that healthy reference samples are needed because of the impact of mortality-selection (Smith & Boesch 2011). Collecting $M_1$Age data from in-vivo wild populations in a non-invasive manner (see Smith *et al.* 2013) is limited due to the constraints of sampling effort.

Many studies have approached interspecific comparisons of dental development on comparisons of the relative pattern of tooth development and emergence, rather than recording absolute timing. Where in vivo studies employing large sample sizes and longitudinal data are often not available or possible, especially among the African apes, $M_1$Age data has been statistically extrapolated from radiographic methods. Histological methods which have allowed $M_1$Age estimates for fossil primates have also been employed to fill in gaps for extant apes, but this results in means derived from 1 to 2 individuals. Because of the above issues with the means, how $M_1$Age varies intra-specifically is often as elusive as how it varies interspecifically. Because the data used for $M_1$Age / ECV regressions is not paired data, it is also not possible to say how these covary intra-specifically at population or individual levels.

Within the sample we do have, there is evidence within some taxa (for instance in *P. troglodytes*) that some of the data used in some calculations of $M_1$Age may not not representative of the species (e.g. it is based on a very limited sample, impacted by wild effect, by mortality biased data, etc). While there are indications of differences in timing between captive and wild populations, between geographic regions, or between subspecies, mean $M_1$Age from sufficient sample sizes are not always available.

The view of fossil hominin diversity is similarly skewed by sampling effort and current variation in suitable exposures of hominin fossil bearing deposits (Maxwell *et al.* 2018). This means that our current view of hominin diversity does not necessarily represent genuine evolutionary signals. With fossil data, uneven sampling is to be expected due to the nature of fossil preservation, can be compounded by the natural uneven distribution of things such as exposed geology, etc. Additionally, sampling of recovered specimens will be impacted by access to the assemblages and and specialised technology. For instance, the cost of transport and access to beam time at a synchrotron radiation facility (see Smith *et al.* 2015) may additionally limit analysis of fossil materials which are naturally a limited resource (e.g. the scarcity of fossil hominin specimens with associated/intact M1, and which died near M1 emergence).

### Section 4.1.1.A Data Aggregation Issues

Some issues arrive when deriving primate data from the literature, especially where it has not been collected or reported for the same contexts in which it is being used. Differences in definitions for the trait being recorded or the group being studied/compared are common. For instance, Leigh (1994) only considered species which devoted over 40-50% of feeding time as ‘folivorous’, while Godfrey *et al.* (2003) used additional anatomy and dietary strategies to include species which are able to rely on foliage during resource crises or which apply dental adaptations to process both seeds and leaves.

When applying quantitative methods to primate data, it can be difficult to aggregate data from varied sources, especially if/where detailed definitions of the traits being recorded are either not available or not cross-compatible. For instance, resources which report LHVs such as “weaning” or “lactation” will have various definitions by which this variable is measured and may not have explicitly defined the terms being applied. It has also been noted that the most appropriate species means estimates should not necessarily be determined by compiling all available data for a species (Smith & Jungers 1997). Research using itemised museum held primate skeletons (and associated field data) has attempted to establish a working base of primate data that future researchers can add to without duplication of data points (Isler *et al.* 2008).

### Section 4.1.1.B Longitudinal vs Cross-sectional Studies

While longitudinal data is more accurate, field studies are often limited in length. The temporal nature of life history variable data, especially in larger bodied species, is of significance. In primatology the length of studies has an impact on sampling because even with year-long studies, supra-annual interval events can be missed (Hawes *et al.* 2013). Because the length of field studies is often limited, collecting longitudinal data may not be feasible, therefore many life history variables have historically been compiled from cross-sectional data out of necessity, which can overestimate ages for life history data (German & Stewart

2002). German & Stewart (2002) noted that while this has been done out of necessity, cross-sectional data can impair the visualisation of adolescent growth spurts, for instance, as it will tend to smooth out growth rate spikes, shorten their duration and flatten the height any spikes still apparent. However, one paper references Dahlberg & Menegaz-Bock in noting that longitudinal data can tend towards later estimations of tooth emergence (Dahlberg & Menegaz-Bock 1958, as cited in Bermúdez de Castro *et al.* 2015). The paper does go on to note that with cross-sectional data the emergence of earlier erupting teeth tend to be based on later cohorts than those of late erupting teeth (Bermúdez de Castro *et al.* 2015).

In human studies, it has been demonstrated that most methods used to predict age based on dental development predict with significant bias (SD 0.86—1.03 yr), can over-age young children, and can considerably under-age older children (Liversidge *et al.* 2010). The method of collection of data is also significant, as studies may group observations by quarter, half, or annual cohorts (e.g. all the children at least 5 yr but not yet 6 yr, or children between 6.75 and 7.0 yr of age), and when this type of data is used, it is important to apply the midpoint of these intervals rather than the minimum age of the group (Liversidge 2003). Reported M1 *emergence* ages can vary in their definitions, reporting initial alveolar eruption (not yet through the gums) or full occlusion. I have preferred the “X, cusp tips half way to occlusal level” age for $M_1$Age which is 5.9 years (Liversidge 2003).

Primate and human dental development data is derived from a number of techniques. Kuykendall (2002) noted that as new techniques have generated more primate dental development information, a number of studies appeared to presume compatibility between data generated by these different means (e.g. histology vs radiography) or data derived from different samples (e.g. living vs skeletal) where said compatibility had not yet been demonstrated via experimental methods. As will be detailed below, this study does use histologically derived ages in an attempt to experimentally include hominids, sub-fossil strepsirrhines and fossil hominoid and hominin species, in order to test the potential impact of a more detailed sample could have on the methods used. Techniques for photographic field studies to more accurately document $M_1$Age in extant hominids show promise (Smith *et al.* 2013).

### Section 4.1.1.C Unmatched and Non-normal Data

Primates $M_1$Age and ECV are left-skewed (not normally distributed) and there are gaps between species groups, due to both variation and sampling effort errors. A cursory look at the scatter plots for $\ln$-transformed and untransformed data reveals visual gaps between the data points, especially between *H. sapiens* and all other extant primates and between hominids and other primates (see Figure 4.1 and Figure 4.2).

Additionally, $M_1$Age data and ECV data are not matched. That is, they are not both compiled from a single study, and the studies compiled are not sampled from identical populations. How these variables correlate at an individual or population group level is not something that can be discerned. In many instances, small groups samples are the only published data available and are treated as representative of the species mean, by necessity. Some species have extensive sample sizes, and others are drawn from a small number of individuals. To detail the situation, the general issues with $M_1$Age and ECV data will be presented separately. For a complete list of which extant species were included in the data set, see Appendix 1.

### Section 4.1.2 $M_1$ Emergence Age

Published dental emergence data for extant primates continues to be limited. When restricted to the $M_1$Age data which could be paired to published ECV, the overall number of extant studies could only be moderately increased compared to previously published studies. This study only has 10 more haplorhine data points (n = 24) than the Smith *et al.* (1995) data set (n = 14), and 5 more haplorhine data points than the Kelley & Schwartz (2012) data set (n = 19). When including strepsirrhines, this study has a total of 33 extant species. This is an increase of only 12 compared to the Smith (1989a) primate data set (n=21). The Smith *et al.* (1995) data set (n=14) is a revised version of that larger data set (n=21) previously published by one of it’s authors (Smith 1989a), which was modified to exclude strepsirrhines, as well as to refine or remove problematic data points where possible (Smith *et al*. 1995).

Many species’ published data isn’t sex-differentiated. In some species, this is because a lack sexual dimorphism makes it difficult to differentiate the sexes.

Therefore, for $M_1$Age, where male and female ages are listed separately, a mean of the two has been employed. Following the established norm, only mandibular $M_1$Age is used. While there is only a slight difference between maxillary (upper) and mandibular (lower) $M_1$Ages, the positive difference between the two increases with body size. It should be noted that some of this data is tenuous, being based on sample sizes as low as n=1 (for instance *Po. p. pygmaeus*). Where two data sets were published, with approximately equal quality, and which can be determined not to be from the same individuals (i.e. there is no duplication), the published $M_1$Ages are averaged (e.g. *G. gorilla*). These parameters have allowed me to include *G. gorilla* and *Pongo pygmaeus* (orangutans) in the data set, but not *Pan paniscus* (bonobos), which will be discussed in more detail below. Without the inclusion of *G. g. gorilla* and *Po. p. pygmaeus*, extant non-human Hominidae would be limited to a single species: *P. troglodytes*. At a minimum, the $M_1$Age is from a published mean of at least n=1.

In previous regressions, *G. gorilla* had been excluded because it's reported $M_1$Age was based on a loosely reported observed age (3.5 yr) and not derived from a mean of recorded ages taken from individuals (Smith *et al.* 1995). However, histologically derived $M_1$Ages for 2 individuals have been published more recently. An $M_1$ histology estimate was produced for a juvenile female *G. g. gorilla,* who had died accidentally (Schwartz *et al.* 2006). An $M_1$Age histology estimate has also been published from a wild shot museum specimen (Kelley & Schwartz 2010). This specimen was donated in 1913 and the available catalog data states that it is and infant skull, with no information on the individual's sex (Cooper & Hull 2017). I have used both specimens, which together produce a mean age of 3.5 yr. While this is still a very small sample size, it aligns with the previously reported age.

A histological estimate age of 4.6 yr for *Po. p. pygmaeus* has been published (Kelley & Schwartz 2010). *Po. p. pygmaues* has been included in this extant primate regression. While this age (4.6 yr) is based on a single individual, the later age is consistent with the reportedly relatively extended development and and life history related variables known for the genus (Winkler *et al.* 1996; Macho & Spears 1999; Wich *et al.* 2004). Larger sample sizes, and employing live wild studies would, of course, be preferred in these two species. However, the larger goal in including more hominids was to determine the possible impact of including more data in the gap in the data that currently occurs between monkeys and extant humans. With currently available data being what it is, what is that impact? It is hoped that future field research will help fill in this data gap, as well as widening our larger understanding of extant hominid and modern human life histories..

There has been debate recently as to whether wild chimpanzee $M_1$Ages are significantly later than reported captive ages. This is following a study of skeletons of wild juvenile *P. t. verus* from Taï Forest, Ivory Coast, Gombe National Park, Tanzania, where a histologically derived $M_1$Age of 4.1 yr for chimpanzees was reported (Zihlman *et al.* 2004). This "wild effect" has been widely cited as being so large as to indicate a widespread underestimate of M1 emergence across extant hominids and/or to require an overhaul of assumptions fossil hominin life history (Monge *et al.* 2007; Kelley & Schwartz 2012). The latter assumes that current regression derived $M_1$Ages for fossil hominins are necessarily accurate. Despite the small sample size for the study, authors have referred to 4.1 yr as the *mean* $M_1$Age for wild chimpanzees. When suggesting that the lower human range (4.7 yr) is approached by the chimpanzee mean for instance (Zollikofer & Ponce de Leon 2010). Others have approached the "wild effect" more conservatively, noting that emergence ages in captive samples may be "slightly advanced" when compared to wild populations, suggesting caution in the application of means calculated only from captive data (Schwartz 2012). Still others have attempted to establish a more accurate wild mean while employing novel field methods, as will be discussed below..

The main problem with dismissing means from captive data sets employing more substantial numbers of observed or calculated ages in favor of the application of a wild chimpanzee mean is that the published "mean" of 4.1 yr now commonly referenced is not entirely correct. It represents the age of the incorrect tooth of an individual. The original sstudy had reported an ***$M_1$Age*** (maxillary/upper), not the standard $M_1$Age (mandibular/lower) used in comparative studies, and which individuals key specimens in the study had belonged had originally been misidentified (Smith *et al.* 2010a). When the Taï Forest specimen was analysed by other researchers to determine the degree of the “wild effect”, the reported mandibular $M_1$Age was nearer **3.7** yr (Smith & Boesch 2011) which would actually place it within the known range reported for captive chimpanzees. Furthermore, the impact of mortality selection was noted: mortality selection was especially pronounced with the youngest individuals and demonstrated a high degree of disease. Because the study employed a small group of mortality selected individuals, the data cannot necessarily be directly compared with reported captive chimpanzee $M_1$Ages, because there is not a comparably reported mortality selected captive peer group to compare this sample with. Additionally, the time during which these individuals died was shown to be one of significantly high infant mortality related to multiple infectious epidemics (Smith & Boesch 2015). Again, even if we accept replacing more appropriately sized captive studies with a single histologically derived age: at either 4.1 for the upper first molar or 3.7 yr for the lower, in a review of multiple published studies for captive *P. troglodytes* molar emergence ages, the specimen still falls **at** or **within** the upper end of the consensus $M_1$Age (upper and lower combined) range of 2.6 to 4.1 yr (Smith *et al.* 2007).

More recently, a photographic field study of life juvenile *P. t. schweinfurthii,* in Kanyawara, Kibale National Park, Uganda, was conducted (Smith *et al.* 2013; Machanda *et al.* 2015). All 5 individuals studied had $M_1$Ages of ≤ 3.3 yr of age (Smith *et al.* 2013). However widely-held primate-wide direct-associations between $M_1$Age and other LHRVs did not hold for the individuals in this study, suggesting the need for further life history studies in hominids with regards to implying the life history patterns of fossil hominins (Smith *et al.* 2013; Machanda *et al.* 2015). A further in vivo study of wild chimpanzee deciduous dentition at Gombe (*P. t. schweinfurthii*) indicates broad similarities in dental development timings between wild and captive conditions (Lee *et al.* 2021). Therefore, with this demonstrated lack of a significant wild-effect when studying healthy individuals in vivo, I have preferred to use the age derived from a large sample of captive individuals for the *P. troglodytes* mean (~3.2 yr; n=38) (Kuykendall *et al.* 1992), which largely aligns with the data for their healthy wild peers (Smith *et al.* 2013) as well as with other captive chimpanzee reports (Nissen & Riesen 1964).

Based on the parameters for inclusion outlined in section 3.2.1 above, I could not include *P. paniscus* in my analysis, as there is no published $M_1$Age for the species, and still only limited published data for *Pan paniscus* dental development. A study of emerged dentition of 5 immature captive *P. paniscus* individuals (deceased), indicated that $M_1$ emergence happened some time before at least 6.74 yr (Bolter & Zihlman 2011). Histology age estimation of the maxillary teeth of a captive (wild-born) *P. paniscus* female with a partially emerged $M^1$, produced[24] a crown formation time which is comparable with that of a *P. troglodytes* $M^1$ (Ramirez Rozzi & Lacruz 2007). In a dental score study, *P. paniscus* appear to have timing of crown and root formation which is largely comparable to *P. troglodytes* (Boughner *et al.* 2012). A recent in vivo study or deciduous teeth emergence including wild *P. paniscus* has demonstrated broad

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[24] based on a 7-9 day periodicity

similarities between P. paniscus and chimpanzees (Lee *et al.* 2021). Given the similarity of *P. paniscus* and *P. troglodytes* crown formation length and timing as well as root formation timing, perhaps an estimated $M_1$Age could have been employed. A very preliminary comparison of $ln - ln$ results indicated limited impact on the degree of correlation between x and y when including an estimated ("dummy") *P. paniscus* value (e.g. with set 1a r=0.96 and with set 2d r=0.87, etc., whether dummy *P. paniscus* was included or excluded). Given the debate over dental timings for wild vs captive chimpanzees (see below), and the potential impact of including two other ape data points derived from extremely small sample sizes (*Gorilla* and *Pongo*), I opted for caution by not including *P. paniscus* at this time. Hopefully future in vivo studies or histology studies will provide a published $M_1$Age for P. paniscus..

### Section 4.1.3 Endocranial Volume

Endocranial volume (ECV) is preferred over brain mass because it is directly compatible with the measures which can be taken for fossil species, but also because it is a more reliable indicator of brain size. This is because the museum collections which can be used to collect measurements represent a considerably larger sample size (Isler *et al.* 2008). The terms endocranial volume, cranial volume, cranial capacity, endocranial capacity, brain volume, brain mass, and brain weight are sometimes employed interchangeably in the literature. When used literally, brain weight/mass are not on a 1:1 scale with ECV. There are equations to calculate volume from mass (see Smith *et al.* 1995). Total ECV is larger than *actual* brain volume because it includes the volume of the space around the brain in its measure.

In some cases, data has been listed as “brain weight” or “brain mass” (grams) for values that were measured as ECV. For instance, the seminal Harvey & Clutton-Brock (1985)Harvey&Clutton-Brock (1985) state that their “Brain Weight (g)” volumetric data (ml) measured from primate crania were converted to weights (g), referencing Clutton-Brock & Harvey (1980). That paper cited the Jerison (1973) work as having covered the 1:1 equivalence of ECV to brain weight. So it can be reasonably assumed that the “Brain Weight” (g) values listed in the widely cited Harvey & Clutton-Brock (1985) *are* ECV (ml) values. Therefore, no correction of the data as reported was needed in said instance. However, the approach to the use of published ECV/brain data from multiple sources must be done with caution, as not all data is directly interchangeable. ECV species means are not taken from the same populations which $M_1$Age is reported from.

Except where otherwise noted, ECV data was obtained from Isler *et al.* (2008). That study provides is a comprehensive and detailed compilation of primate wild specimen ECV measurements, with supplemental materials detailing the individual specimens used, listed by museum accession numbers. This allows future researchers to use this with potential future specimen measures while avoiding any duplication of data. A small handful of the ECV values they listed included species means taken from Harvey & Clutton-Brock (1985). Of those species, only one species is included in this study: *S. nigricollis.* However, I have preferred the mean from Smith *et al.* (1995) for *S. nigricollis*.

Unless otherwise specified, ECV data is from wild specimens (see Appendix 1). If published ECV data was not found for a species in order to match a published species mean $M_1$Age, that species was not included. However, given the nature of how ECV is easily measured from museum specimens, the tendency was for there to be more species ECVs available than published $M_1$Ages to pair them with. For this reason, there also tended to be more available ECV means which included, or were solely derived from wild specimens than is the case for the published $M_1$Age means.

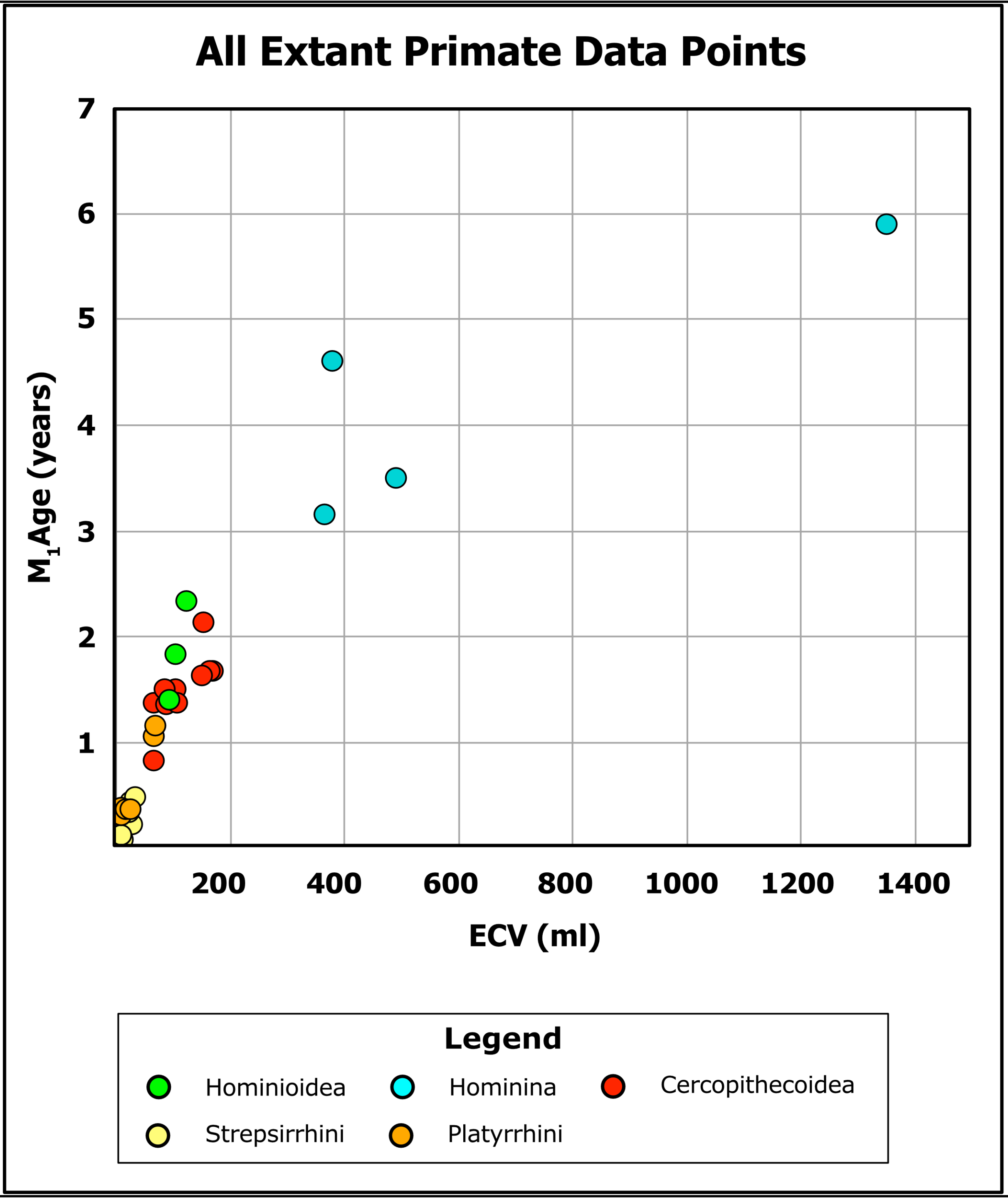

**FIGURE 4.1 SCATTERPLOT: PRIMATE (EXTANT ONLY)**

Scatter plot (no regression) of all of the extant Primate data points.

This plot is presented to demonstrate the issues with "gaps" between extant data available for monkeys, hominids, and *Homo sapiens.*

Regressions are presented in Chapter 5.

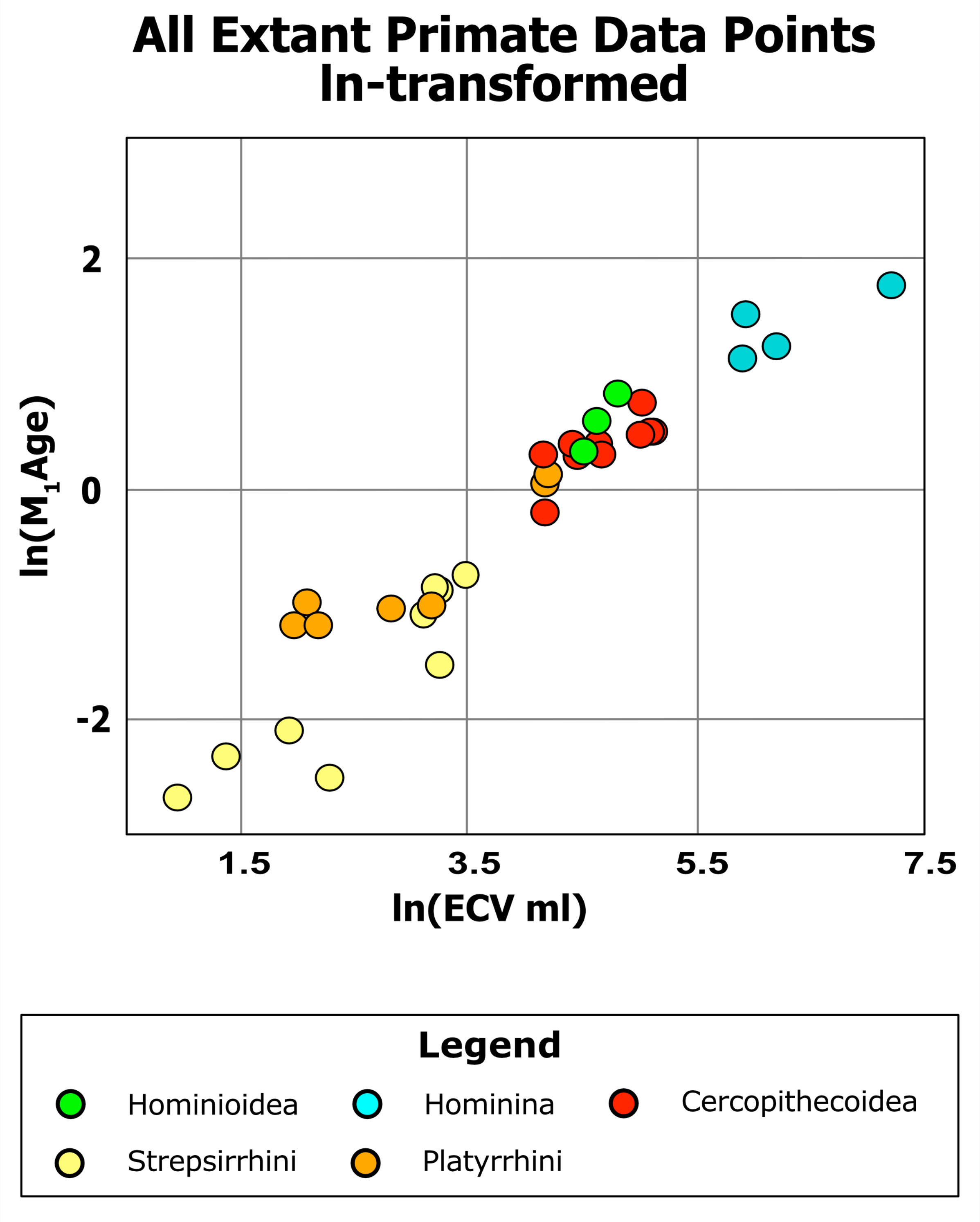

**FIGURE 4.2 SCATTERPLOT: ln-TRANSFORMED PRIMATE (EXTANT ONLY)**
Scatter plot (no regression) of all of the ln-transformed extant Primate data points. This plot of the ln-transformed extant Primate data points is presented to demonstrate where "gaps" are still evident between groups after transformation of the data. Regressions are presented in Chapter 5.

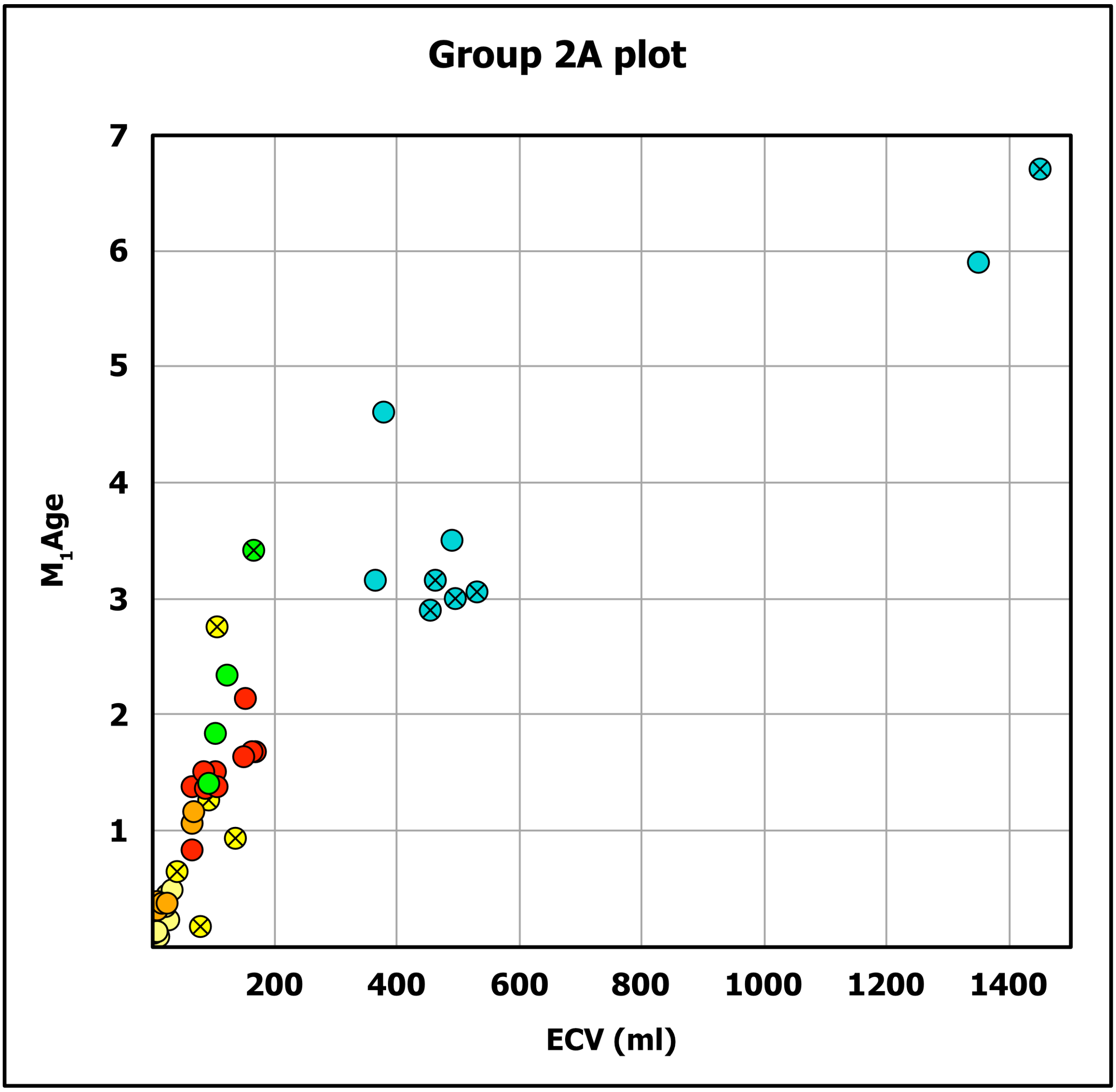

**FIGURE 4.3 SCATTERPLOT: PRIMATE (EXTANT & EXTINCT)**
Scatterplot (no regression) of all the extant and extinct Primate data points.
This plot is presented to demonstrate the where gaps appear in the data set between monkeys, hominids, and *Homo sapiens* in the available primate dataset when extinct species are included alongside the extant species.
Regressions are presented in Chapter 5.

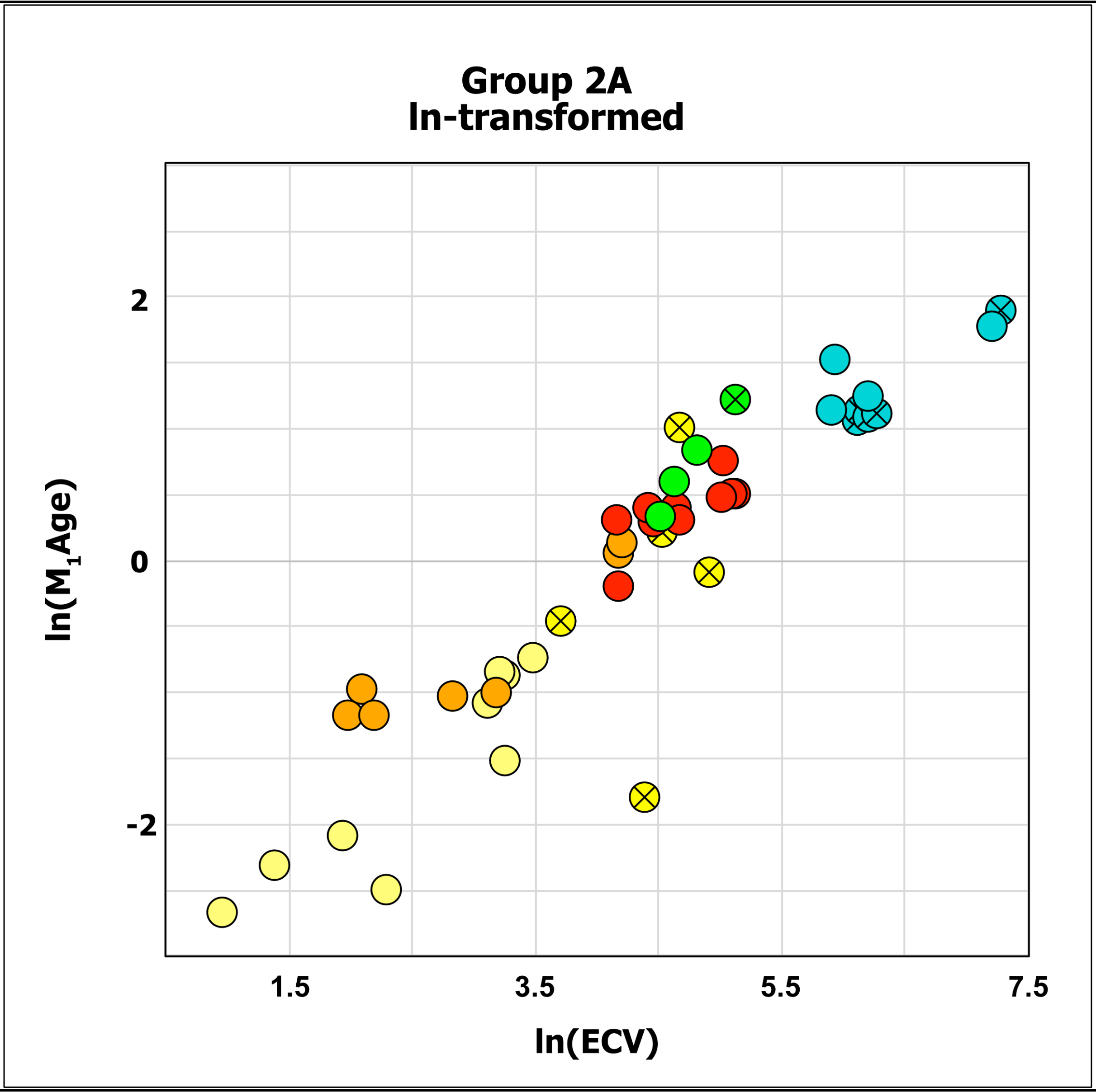

**FIGURE 4.4 SCATTERPLOT: ln-TRANSFORMED PRIMATE (EXTANT & EXTINCT)**

Scatter plot (no regression) of all of the ln-transformed extant and extinct Primate data points.

This plot is presented to demonstrate the where gaps appear in the data set between monkeys, hominids, and *Homo sapiens* in the available ln-transformed primate dataset when extinct species are included alongside the extant species.

Regression plots are presented in Chapter 5.

### Section 4.1.4 Extinct Species

Three types of extinct species were included: Sub-fossil lemurs, fossil Miocene Apes, and fossil Hominins. I will present groups sequentially, beginning with the lemurs. Sub-fossil lemurs are interesting because these recently extinct lemur species filled dissimilar niches to many of the extant species which survived following the relatively recent human settlement of Madagascar. Five sub-fossil lemur species were found with pair-able published $M_1$Age and ECV data (see Appendix 2). All of these species are considerably larger in body size than the extant lemurs in this study. The largest extant lemurs in this study are *Propithecus verreauxi* and *Varecia variegata,* both with means of 3.5 kg. The smallest Strepsirhines weigh as little as 213g. Estimated body mass for the sub-fossil lemurs range from 11.3 kg for *Mesopropithecus globiceps,* up to 85.1 kg for Megaladapis edwardsi (Catlett *et al.* 2010). The largest species do not necessarily demonstrate slower dental development rates and some tend to diverge from the strong correlation found in extant Primates. $M_1$Ages range from 0.2 to 3 yr and the latest $M_1$Age belongs to *Hadropithecus* which is estimated to have weighed only 35.4 kg (Catlett *et al.* 2010).

Because there is a relative lack of extant ape species compared to the number of non-ape primate species, so the potential of adding extinct Miocene apes to the study was explored. Unfortunately, because of the sparse fossil record for these apes, there are very few $M_1$Ages for this grou*p.* In some instances, there were only CFT calculations were available for some species (Mahoney *et al.* 2007). Published $M_1$Ages were found for only 4 species, and only

*Ekembo (Proconsul) heseloni* could be paired with a matching published ECV (Benyon *et al.* 1998; Alba 2010). In the case of published $M_1$Age data for *Hispanopitchecus laietanus*, only the ECV for another species in the same genus, *H. hungaricus,* was located (Alba 2010; Dean & Kelley 2011). However, the estimated body size data for each was dissimilar enough to not feel comfortable with pairing their ECV and $M_1$Age  for the purposes of this regression (Alba *et al.* 2012).

There is a published histology estimated $M_1$Age (6.7 yr) for *H. neanderthalensis* (Macchiarelli *et al.* 2006). To build the regressions, I have used the *H. neanderthalensis* data point in the Set 2 (Extant & Extinct) models, but not the *H. erectus* data points, which is being used as the main test for accuracy. This is in order to avoid "circularity" in the calculation. Historically, age estimates for fossil hominin specimens have been built via circular approaches out of necessity, but methods are being developed to avoid this (Smith *et al.* 2015). Additionally, when small sample size models are assessed with the same sample that they are built with, this will provide a view of *apparent* accuracy, rather than actual accuracy (Bean *et al.* 2012). It also can allow for asking whether pred-$M_1$Age is more often accurate for a fossil hominin $M_1$Age used to construct a model than for a fossil hominin $M_1$Age not included in the model. Paleoanthropology will continue to have hominin specimens/species for which histological $M_1$Age determination is still not possible. Therefore, what is emphasised in this study is: can regression(s) be created which can be verified for predictive accuracy when applied to a hominin species which itself was not included in the *creation* of said equation. Luckily another *Homo* species was available, so that the fossil data wasn't relying solely on Australopiths to represent fossil hominins.

### Section 4.1.5 ECV Data for Fossil predictions

I compiled fossil hominin ECV from over a dozen species. In cases where there were less than at least 3 individuals, the species were excluded. Some individual fossils which appear to be significant outliers for ECV or site age were also excluded.

In terms of the test mean of *H. erectus*, my total mean is slightly different from the *H. erectus* mean from Smith *et al.* (1995), presumably due to the more recent African *H. erectus* fossil ECVs recorded since 1995. I couldn't ascertain specifically which exact specimens my mean differed from their means by. Smith *et al.* (1995) used Rightmire (1986) and Wood (1991) for the 2 means provided for African *H. erectus* cranial capacities. I was unable to access Rightmire (1986), however I did access Rightmire (1981) and Rightmire (2004), and have tried to piece together the likely data points involved in the African *H. erectus* mean of 862 ml reported in Smith *et al.* (1995) for Rightmire (1986), by comparing Rightmire (1981) with Rightmire (2004) and also removing any specimens that were not yet known before 1986. It appears that Rightmire's mean included the *H. ergaster*. I mention this because Smith *et al.* (1995) mentions that Wood's (1991) 826 ml mean represents specimens identified as

"*Homo* aff. *H. erectus* (= *H. ergaster*)." Possibly Wood's (1991) mean used the same individuals but the value published was transposed? Nevertheless, the mean value of the African *H. erectus* ECVs included here is 883 ml alone, or 858 ml if the *H. ergaster* group is included.

The Smith *et al.* (1995) Asian *H. erectus* ECV mean of 983 ml was close to my mean of 981 ml for the Asian fossils excluding the Ngandong specimens (which are treated as *H. soloensis*). If Ngandong were to be included, the mean would instead be 1026 ml.

## Section 4.2 Regression Methods

The primary question addressed by this thesis is whether accurate $M_1$Age for fossil *Homo* species (with specific focus on *Homo erectus* s.l.) can be predicted from primate $M_1$Age and ECV data is a reasonable approach to predicting the $M_1$Age emergence age for *Homo* species*,* which are polytypic in terms of ECV and which relative outliers—as Primates—in terms of both body and brain size. Above, the question of whether currently available published Primate data might expand the data set was addressed. This section will address applying regression models to the increased data set.

Martin (2003) points out that issues can arise with the primate data in parametric line-fitting procedures in that the data violates requirements of those methods: x cannot be measured without errors, and there isn't certainty that the y value in a correlation is directly dependent on the x value. Martin (2003) suggests that a minimal response to these potential sources of error would be to apply different line-fitting techniques and examine their effects on the results obtained. He also notes that where grades exist within the data set, individual best fit lines should be calculated for each grade, rather than a single best fit line for the set as a whole (Martin 2003). Because grades within a dataset should have individual best fit lines, taxonomic groups should be tested within the data set to determine if grade differences exist among them (Martin 2003).

The questions are not designed to explore how the Primate order varies *in itself.* Nor do they attempt to re-establish the correlation between $M_1$Age and

ECV (though correlation is addressed). The research questions specifically address the various factors that impact the performance of regression predictions in this specific application towards fossil hominin life histories. The aim is to determine whether primate data used in this manner produces possible/probable $M_1$Age means. The questioning will be staged as follows:

- When applied to an updated *H. erectus* ECV mean, with an updated primate data set, does this type of regression create accurate predictions?
- Increased extant data points, especially within hominids?
    - Adding extinct data points (i.e. histologically derived $M_1$Age)?
    - Excluding additional specific taxonomic groups from the model?
    - Applying the residuals from *P. troglodytes* or *H. sapiens* predictions to the *H. erectus* predicted value?
- Is another type of regression as useful or more useful than least-squares regression using two-sided $\ln$-transformed data?
- Does sample size/population segment to which the predictions are applied impact the accuracy of the predictions?

To address the above questions, ordinary least-squares regressions using two-sided $\ln$-transformed data were performed. These were repeated using progressively exclusionary taxonomic groupings. The same processes were repeated with the data points of a small number of extinct taxa. Then all of this was repeated using cubic, quadratic and least-squares linear regressions using non-transformed data. This process created 40 regression models.

To simplify discussing this many equations, the datasets are defined in 5 groups by their taxonomic level: Primates (Group A); Haplorhine (Group B);

Catarrhine (Group C); Hominoid (Group D); and Hominid (Group E). Those 5 groups are first performed with only extant primate species (Set 1) and then repeated with extinct species added (Set 2). See Table 4.1 for a chart of the names. Because this process created at least 40 regressions, I established criteria for which models would be explored in more in-depth discussion, which is outlined in more detail, later, in Section 4.2.2.

**TABLE 4.1 DATA SUBSET GROUPS**

| | SET 1 | SET 2 |
|---|---|---|
| Primates (A) | 1A | 2A |
| Haplorhini (B) | 1B | 2B |
| Catarrhini (C) | 1C | 2C |
| Hominoidea (D) | 1D | 2D |
| Hominini (E) | 1E | 2E |

### Section 4.2.1 Equation Models:

Bivariate regressions attempt to produce a line which best predicts the value of Y (the dependent variable) from X (the independent variable). A linear model regresses the dependent on the independent variable. Least-squares criteria finds the y-intercept and slope that best minimise the mean of the squared errors (Myers & Well 2003). Linear models regress Y on X, producing this form of the equation:

$$Y_i = b_0 + b_1 X_i.$$

where Y is the dependent value, X is the independent value, and $b_0$ (intercept) and $b_1$ (slope) are the least squares coefficients. Where data isn't distributed linearly, transforming one or both sides of the data in a linear least-squares regression model can achieve approximate linearity (Stimson *et al.* 1978). In primates, where there is a wide spectrum of body mass, which many traits correlate with, both sides can be left skewed. Using $\log$ or $\ln$ to transform both sides is the commonly applied method in paleoanthropology, and was the method used in Smith *et al.* (1995).

In order to explore whether other models can predict accurately for fossil hominins, additional regression methods were used. In a preliminary exploration, I applied all of the options available for regression "curve estimation" in SPSS Statistics. Polynomial models also appeared to fit the non-transformed values produced similarly high correlation values. Polynomial models regress Y on powers of X (Ostertagová 2012). Cubic, quadratic, and linear models were chosen for the non-transformed data. Polynomial models produce equations in this general form

$$Y = b_0 + b_1x + b_2x^2 + \ldots b_nx^N$$

Quadratic models are in this form:

$$Y = b_0 + b_1x + b_2x^2$$

Cubic models are in this form:

$$Y = b_0 + b_1x + b_2x^2 + b_3x^3$$

Polynomial regression is multiple regressions where the additional variables are not separate independent variables, but increasing powers of x. Polynomials can be used to approximate an unknown curvilinear relationship (DeCoster & Claypool 2004).

### Section 4.2.2 Creating Regression equations

As stated above regression analyses were performed on the primate data set in groups which progressively excluded points taxonomically. For each of these groups, four equation types were employed: $\ln$-transformed, polynomial (Cubic and Quadratic), and linear regressions.

As noted above, primate $M_1$Age and ECV plots are skewed. In primatology and paleoanthropology, two-sided $\ln$-transformed regressions (hereafter $\ln$-transformed or $\ln$-$\ln$) or two-sided log-transformed regressions are frequently employed, as they can be used to address skewed and non-linear data (Smith *et al.* 1995; DeSilva & Lesnik 2008; MacLean *et al.* 2009; Smith 2009; DeSilva 2011; Kelley & Schwartz 2012; Smith *et al.* 2017). However, one of the common "sins" of regression analysis is not considering other models (Freckleton 2009). Polynomial regression is another method which can be employed when the relationship between the dependent and independent variables may be curvilinear rather than linear. In an initial exploration of available regression methods in SPSS, cubic or quadratic equations also appeared to plot well for *H. sapiens*. For comparison with the above methods, I chose to employ cubic and quadratic regressions.[25] These were performed in the same manner—using the groups and methods noted above for $\ln \bullet \ln$ regressions.

| | **Stage 1** | **Stage 2*** |
|---|---|---|
| r | ≥ 0.80 | |
| p | ≤ 0.001 | |
| Predicted $M_1$Age In Range/Accurate | ±0.5 | ±0.2 |

**Table 4.2 Inclusion Criteria Summary (in stages)**
* - after correction with *P. troglodytes*- or *H. sapiens*-residual

### Section 4.2.3 Inclusion criteria for further examination

The procedures noted above generated 40 equations. In order to have a manageable amount of equations for further analysis, I developed performance criteria for fit and inclusion (summarised in Table 4.2). Equation models needed to be a good fit for the data being used, and to continue to show a high degree of positive correlation, so the cut off for inclusion was a combined r ≥ 0.80 and p ≤ 0.001. This initially excluded 10 equations. The remaining models were included if their test prediction values for *P. troglodytes, H. sapiens*, and *H. erectus* were within ±0.5 yr of their observed values. The predictions are not

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[25] I remain cognisant, however, that this should be an exploration, rather than an exercise which runs the risk of "overfitting", which is another of the "sins" of quantitative analysis (Freckleton 2009).

being judged on whether they fall within the full range of $M_1$ emergence for those species. The regression models produce a *species* value (i.e. the model is built on a mean $M_1$Age and ECV value for each species used, not on the ranges for those species), and the predictions are judged based on their accuracy to predict a *species* value, not an individual variation within the species range.

For the second stage criteria, "adjustments" were applied to the *H. erectus* predictions produced by each model. Each residual-adjustment employed the chimpanzee- and human-residuals from that particular prediction's model. Models which fall within the stage one range criteria (hereafter **RC**) for *H. erectus* after adjustment are noted. Where predictions for *H. erectus* were improved to within ±0.2 of observed after correction with either residual are considered to meet the second stage criteria. Some models which do not meet the first or second stage criteria are included for comparison with models which met inclusion criteria (by model Group).

The results for the stage tests for all models are included within the appendices. Where anything hasn't been covered in greater depth, therefore, either it did not identify an instance of regression accuracy or else was largely similar to a result which is discussed in detail. As a follow up, the predictions for three key fossil species/groups were produced and where they met stage 1 or stage 2 was noted (see Table 4.3 for list). The follow up predictions were not used to screen out models for discussion, but are used to analyse points where predictions which are accurate for *H.erectus* might not be accurate for other fossil hominins. As the goal is a model which has been tested for observed $M_1$Ages to the extent where one can be confident using it for predictions with newly discovered fossil hominin populations or identifying areas for caution in the application of these models.

| | **$M_1$AGE (YEARS)** | **ECV (ML)** |
|---|---|---|
| *P. troglodytes* | 3.2 | 365 |
| *H. sapiens* | 5.9 | 1350 |
| *H. erectus* | 4.4 | 935 |
| Australopith group | 3.0 | 470 |
| Fossil *H. sapiens* | 5.9 | 1486 |
| *H. neanderthalensis* | 6.7 | 1442 |

**TABLE 4.3 OBSERVED HOMINID DATA, KEY SPECIES**

### Section 4.2.4 Adjustments with residuals

In biology, there is an assumption that variation from the line of regression is non-random. Smith *et al.* (1995) used this assumption to apply residuals to make adjustments to fossil hominin $M_1$Age predictions. Where humans or chimpanzees vary from the haplorhine norm, for instance, we might see that a fossil hominin varies in the same way. By adding the residuals for *P. troglodytes* or *H. sapiens* to the predicted value for *H. erectus* before performing de-transformation on the value, they provided estimates for the range of what *H. erectus* could have been within, if it had also deviated from the expected value for haplorhines in the same way as either species and labeled these values as

"Chimpanzee-like" or "Human-like" (Smith *et al.* 1995). This same process is used in this study, to examine is adjustment with these residuals reduces the absolute residual of the predictions for *H. erectus,* and also to examine whether apparent improved accuracy for *H. erectus* is applicable to other fossil hominins, however the terms "___-like" are not used in this study. This is to avoid confusion with studies which use "___-like" terms when comparing fossil hominins variable values to observed human and non-human ape variable to determine which group the fossil hominin value falls metrically closest to. In contrast, the usage when comparing residuals refers to the manner in which individual observed values vary in distance above or below the line of regression. Two values can vary from the line by a similar distance, while the values are still distant from each other. For instance, in Model Linear-1B, the *C. jacchus* and *S. syndactylus* residuals are both ~0.5, while their predicted $M_1$Age[26] values = 0.3 yr and  = 2.3 yr, respectively.

After creating the equations and the test species predictions noted above, I applied the *P. troglodytes*-residual[27] and *H. sapiens*-residual[28] from each model to that model's *H. erectus* mean prediction value and noted how this changed each pred-$M_1$Age value.[29] I noted where this adjustment brought *H. erectus* into the ±0.5 range of the observed mean. The unadjusted pred-$M_1$Age values for regional sub-groups of *H. erectus* were within ±0.5 of the S7-37 histology

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[26] hereafter pred-$M_1$Age

[27] hereafter *P*-residual

[28] hereafter *H*-residual

[29] hereafter any residual adjusted pred-$M_1$Age will be referred to as *H*a-$M_1$Age (*H*-residual-adjusted-pred-$M_1$Age) or *P*a-$M_1$Age (*P*-residual-adjusted-pred-$M_1$Age).

calculated $M_1$Age estimate which is being employed in this exercise as a mean for *H. erectus*. I also noted where (if pred-$M_1$Age is already within RC) this adjustment reduces the absolute residual of the pred-$M_1$Age value for *H. erectus*, and where that reduction brought it within ±0.2 of the observed value. As the unadjusted pred-$M_1$Age values for mean African *H. erectus* $M_1$Age in Smith *et al.* (1995) were within ±0.2 of the (now) observed value for *H. erectus*, this appears to be a reasonable cut off for determining if regressions continue to predict accurately for *H. erectus* given a change in ECV means/range for the species, an increased primate data set N, and the available S7-37 histologically derived $M_1$Age.

### Section 4.2.5 Predictions for Fossil Hominin specimens

Fossil hominin ECVs can vary greatly between individuals and populations (see Section 2.4). ECV for modern *H. sapiens* can range significantly from our species mean of ~1350: from 907 ml up to 1786 ml (Lewis *et al.* 2011). ECVs reported for *Homo erectus* s.l. (including proposed sub-species and paleo-demes) specimens range from 546 to 1251 ml and means for the species as a whole, as well as for various population groups, can vary depending on which individual ECVs are included/excluded when generating a group or species mean (see Appendix 4.c).

This thesis is asking whether regression model can generate reasonably accurate predictions for fossil hominin populations. To this end, using the equations selected for further analysis, predictions were generated for individual fossil hominin specimens from a number of species to generate means, ranges, and graphs. The list of specimens for which predictions were generated can be found in Appendix 4.c and the results are presented in Chapter 6. The species represented by these fossil specimens include: *A. afarensis*; *A. africanus*; *P. boisei; P. robustus*; *H. habilis* s.l.; *H. e. georgicus*; *H. e. ergaster*; *H. e. erectus*; *H. soloensis*; *H. heidelbergensis*; *H. antecessor*; *H. neanderthalensis*; fossil *H. sapiens*. This list is not exhaustive of all known fossil hominin ECVs, and some specimens or species have been excluded if they appear to be potential outliers (for their species, region, or time period) or if there are significant issues with dating, or where there are too few reported ECVs for a species, etc. For instance, the Gongwangling adult female cranium has been excluded because it is significantly earlier than the other Chinese crania, the skull is described as more primitive, and the ECV is considerably smaller and within the range of Dmanisi hominins (Rukang & Xingren 1985; Antón 2002b; Dennell 2009).

The species are grouped as follows:

- Australopiths (*Australopithecus* and *Paranthropus* species)
- Early *Homo* species (*H. habilis* s.l., *H. e. georgicus*, *H. e. ergaster*)
- *H. e. erectus* (in regional sub-groups: African; East Asian; Southeast Asian)
- Middle Pleistocene *Homo* species
- Late Pleistocene *Homo* species

In instances where two reported ECVs exist for the same specimen, I have generally chosen the most up to date reassessment of ECV, where the source is published, available, and details the methodology which led to the reassessment of the ECV. I have placed the Ngandong materials in *H. soloensis,* with the Middle Pleistocene *Homo* species, based on their geological age. This should not be taken as a full assessment of them as a separate species, but as an acknowledgement of their anatomical and temporal difference to the Sangiran and Trinil *H. erectus* materials. Similarly, *H. e. ergaster* and *H. e. georgicus* have been grouped with Early Pleistocene *Homo* species Some consider them part of the *H. erectus* s.l., others as separate species, others as subspecies or paleo-demes of *H. erectus*. This isn't meant to be taken as defining of those fossils, but in aid of visualising how treating these fossil populations a sub-species impacts the assessments made of their life histories when regressions are applied to them.

Again, the fossil ECVs used is not a definitive list of known fossil hominin cranial materials. It is used as a reasonable estimate of the ranges for these species in order to explore how the different equations handle an array of fossil hominin cranial variation. When discussing the results, I have made a point to refer to regression results as *predicted* $M_1$Age[30], which is different to *observed* $M_1$Age: prediction value is an artefact of any given chosen regression method (and ad hoc adjustment) as opposed to a value calculated from observed values reported in field/dental studies. The equations used for the predictions for this stage are noted in Chapter 5. Fossil hominin pred-$M_1$Age box plots are presented

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[30] i.e.: pred-$M_1$Age, *H*a-$M_1$Age, or *P*a-$M_1$Age

in Chapter 6. The results from Chapters 5 and 6 will be subsequently discussed in Chapter 7.

# Chapter 5

# Chapter 5  Regression Model Results

This chapter presents the results of the various regressions which are set out in Chapter 4. The regression models will be presented in two sections, by Set.[31] Within the 2 Sets, the model results are presented in subsections by Groups.[32] Using this study's Primate data set (described in Chapter 4), four types of equation were performed, creating 40 regression models. The results of selected models are presented within each Group section, by model subsections in the following order:

- two-sided ln-transformed data ("ln-" )
- untransformed data:
    - third degree polynomial ("Cubic")
    - second degree polynomial ("Quad")
    - linear regression ("Linear")

Each model will be referred to by the above equation type followed by set number and group letter (e.g. ln-1A, Cubic-2B, etc.).

The regression plots are presented in figures at preceding each model subsection, and comparative and summaries in tables at the end of Group section. Only the graphs of the selected models in detail are presented within the text. Regression plots for all models can be found grouped together by equation type in the Appendices. The text here will provide a summary of model fit and correlation, with some comments on any major notable differences. These

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[31] For reference: Set 1. Extant only; Set 2. Extant & Extinct

[32] For reference: A. Primate; B. Haplorhine; C. Catarrhine; C. Hominoid; and E. Hominid

differences or any other issues arising from these results will be discussed further in Chapter 7.

Nearly all of the 40 models demonstrated a very high positive correlation ($r \geq 0.90$). The only model returning a value that wasn’t at least a high positive correlation ($r \geq 0.80$), was excluded by $p > 0.001$. The models that did not meet this criteria were from either Group D (Hominoid) or Group E (Hominid), and this is probably an artefact of the very small sample sizes of theses datasets ($n < 10$). No model demonstrated normal distribution.

A majority of the models’ *H. erectus* pred-$M_1$Ages have residuals greater than ±0.5. That is, over- or under-predicting by more than 6 months (27 out of 40). The majority of the Group A, B, and C models over-predicted for *H. erectus.* Between the second and third degree polynomial models, the Cubic performed better for Set 1 groups, and Quadratic performed better for Set 2 groups.

## Section 5.1 Set 1 Models (Extant Only)

This section (Set 1 Models: Extant Only) and the next section (Set 2 Models: Extant & Extinct) are presented as subsections by order of taxonomy grouping from least restricted (Group 1A: Primate, Extant Only) to most restricted (Group 1C: Catarrhine, Extant Only). Of the Set 1 (Extant Only) models, only the Group-1A, -1B, and -1C models pass the Stage 1(a) criteria. These groups are presented here in three sections. In the Set 1 (Extant Only) models, the third level polynomial equations (Cubic models) performed better than the second level polynomial equations (Quad Models). Therefore, this section presents just the the $\ln$-transformed, cubic, and linear models (in that order) within each Group's subsection.

Each model's regression plot precedes it's section heading so that when viewed in book format, the plot should appear on the left (even) page, next to the first page of the model's text on the right (odd) page. Summary tables comparing key hominid species $M_1$Age predictions between the models within each Group is presented at the end of each Group subsection (after each linear model text).

Not all of the models presented predict *H. erectus* within RC[33], but are included for comparison. The following models predict *H. erectus* within RC: Cubic-1A, -1B, and -1C; Linear-1C. The following models predict *H. erectus* $M_1$Age within RC only after adjustment with the *H*-residual: $\ln$-1A, -1B, and -1C; Linear-1A, and -1B. Only Cubic-1B, Cubic-1B, Adjusted-$\ln$-1A, and Adjusted-

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[33] range criteria = observed $M_1$Age ± 0.5 years

Linear-1C predict *H. erectus* $M_1$Age within Stage 2 accuracy criteria (hereafter **AC**). The regression plots for all 40 models can be found in the Appendices.

### Section 5.1.1 Group 1A (Primate, Extant Only)

This section will now present the models built from Group 1A (Primate, Extant Only). This is the group that employs all of the extant data points. Only one model meets all Stage 1a and is within RC (see Section 4.2.3 above): Model Cubic-1A. Model ln-1A and Model Linear-1A both meet the initial criteria only after adjustment with that model's *H*-residual. Adjusted-ln-1A predicts *H. erectus* $M_1$Age within AC.

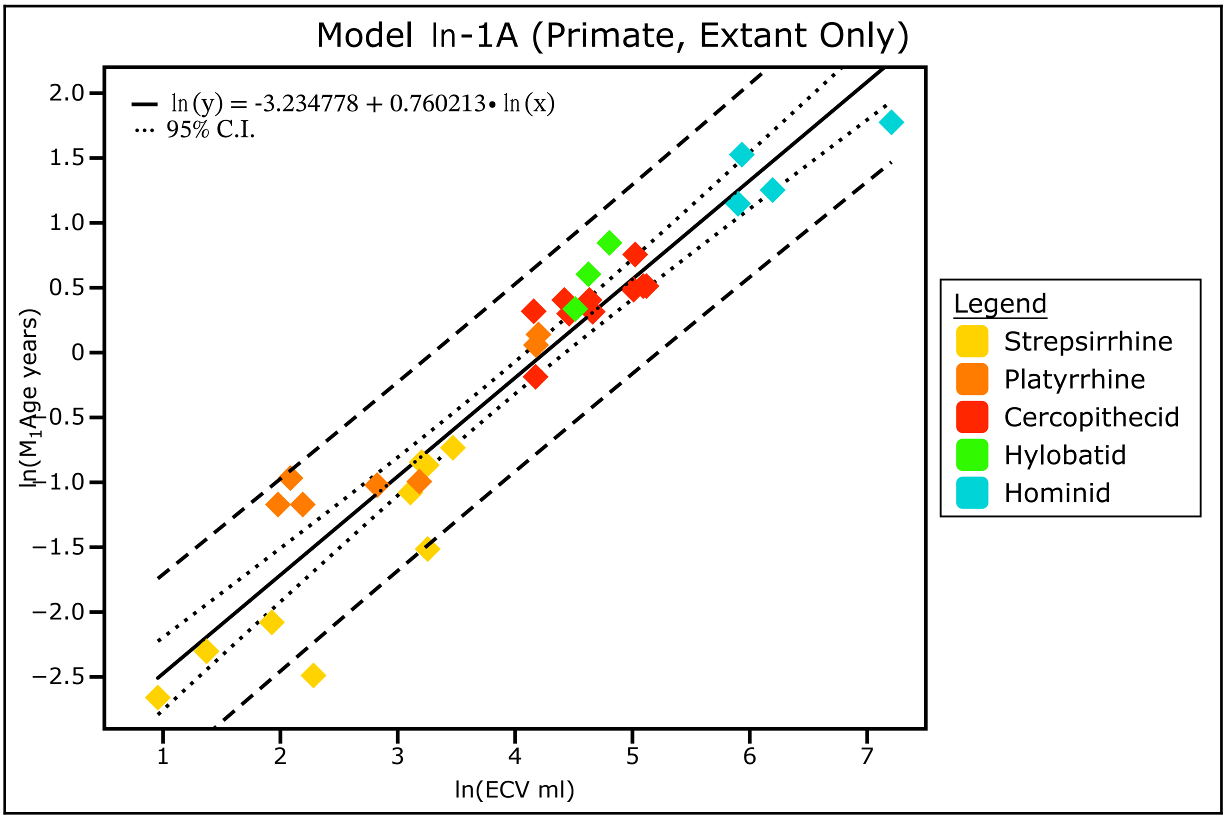

**FIGURE 5.1 REGRESSION PLOT: ln-1A (PRIMATE, EXTANT ONLY)**

Model ln-1A (Primate, Extant Only): ln • ln scatterplot for the extant primate sample (derived from 33 primate species; $r = 0.96$, $r^2 = 0.92$, $p < 0.001$, $s_e = 0.349$). Solid line represents the regression line, where y is $M_1$Age (years) and x is ECV (ml). Dotted lines represent the upper and lower 95% confidence intervals.

Model ln-1A predicts the three key hominids $M_1$Age as follows: *H. erectus* = 7.1 yr; *H. sapiens* = 9.4 yr; *P. troglodytes* = 3.5 yr. Only after adjustment with the *H*-residual does Model ln-1A predict *H. erectus* $M_1$Age within AC.

Within the ln-transformed Set 1 (Extant Only) models, the coefficient of determination is greater in Model ln-1B (Haplorhine). Within the Group-1A models, the coefficient of determination in the second level polynomial (Cubic) is greater than in the ln-transformed and Linear models.

### Section 5.1.1.A Model ln-1A (Primate, Extant Only)

Model ln-1A (Primate, Extant Only) was created applying a linear regression to the two-sided ln-transformed data using the extant primate species. Model ln-1A produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y) = -3.234778 + 0.760213 \bullet \ln(x)$$

Model ln-1A has a very highly positive correlation ($r=0.96$, $p<0.001$, $s_e=0.349$). Model ln-1A pred-$M_1$Ages are as follows: *H. erectus* = 7.1 yr, *H. sapiens* = 9.4 yr, and *P. troglodytes* = 3.5 yr. The pred-$M_1$Age for *P. troglodytes* is within RC, while the pred-$M_1$Ages for *H. erectus* and *H. sapiens* are over-predicted. The pred-$M_1$Age is over-predicted in the other three fossil hominins.

In model ln-1A*,* the *H*-residual = -0.469*,* and *P*-residual = -0.103. Applying the *H*-residual produces an *H*a-$M_1$Age for *H. erectus* = 4.5 yr, which is within AC. The *H*a-$M_1$Age values for the other fossil hominins as follows: Fossil *H. sapiens* = 6.3 yr; *H. neanderthalensis* = 6.2 yr; Australopiths = 2.7 yr. Therefore, the *H*a-$M_1$Ages for the other fossil hominins are within RC, but outside of AC. The *P*a-$M_1$Ages for *H. erectus* and the other fossil hominins are also outside AC. Model ln-1A does not meet the stage one criteria.

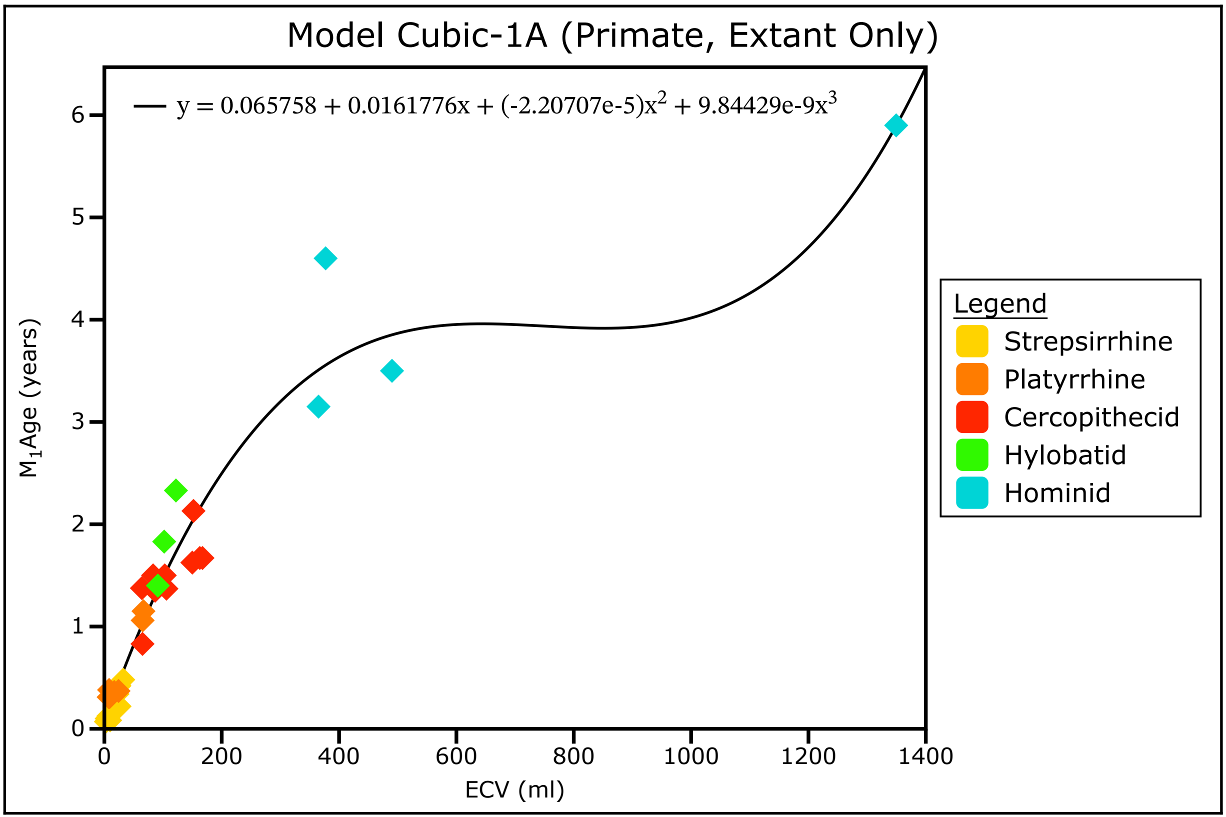

**Figure 5.2 Regression Plot: Cubic-1A (Primate, Extant Only)**

Model Cubic-1A scatterplot for the extant primate sample (derived from 33 extant primate species; ($r = 0.97$, $r^2 = 0.94$, $p < 0.001$, $s_e$=0.318).

Solid line represents the third level polynomial equation regression, where y is M$_1$Age (years) and x is endocranial volume (ml).

Model Cubic-1A predicts M$_1$Age as follows: *H. erectus* = years; *H. sapiens* = years; *P. troglodytes* = 3.5 years.

Dashed lines represent trend lines by taxonomy.

Within the Cubic Set 1 models, the coefficient of determination is greatest in both Models Cubic-1A (Primate) and Cubic-1B (Haplorhine). Within the Group 1A models, the coefficient of determination in the second and third level polynomials is greater than in the ln-transformed and linear models.

## Section 5.1.1.B Model Cubic-1A (Primate, Extant Only)

Model Cubic-1A (Primate, Extant Only) was created using a third degree polynomial regression with the extant primate species data points. Model Cubic-1A produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.065758 + 0.016178x - 0.00002207x^2 + 0.000000009844x^3$$

Model Cubic-1A has a very highly positive correlation ($r = 0.97$, $p < 0.001$, $s_e = 0.318$). Model Cubic-1A pred-$M_1$Ages are as follows: *H. erectus* = 3.9 yr, *H. sapiens* = 5.9 yr, and *P. troglodytes* = 3.5 yr. The pred-$M_1$Ages for *H. erectus*, *H. sapiens*, and *P. troglodytes* are all within RC. Therefore, Model Cubic-1A meets the Stage 1 inclusion criteria for further discussion (as defined in Methods). Cubic-1A pred-$M_1$Age for the remaining hominins as follows: fossil *H. sapiens* = 7.7 yr; *H. neanderthalensis* = 7.1 yr; Australopiths = 3.8 yr. Therefore, pred-$M_1$Age for *H. neanderthalensis* is within RC, while Fossil *H. sapiens* and the Australopiths are over-predicted.

In Cubic-1A, the *H. sapiens* $M_1$Age residual = -0.003, and *P. troglodytes* $M_1$Age residual = -0.359. Due to the nature of the Cubic Models, the *H*-residuals are too small to bring predicted $M_1$Age for *H. erectus* into AC, and the *P*-residuals reduce the prediction for *H. erectus* to below AC. Therefore residuals are not applied with Model Cubic-1A. Model Cubic-1A (Primate, Extant Only) meets the Stage 1 criteria for inclusion in Chapter 6.

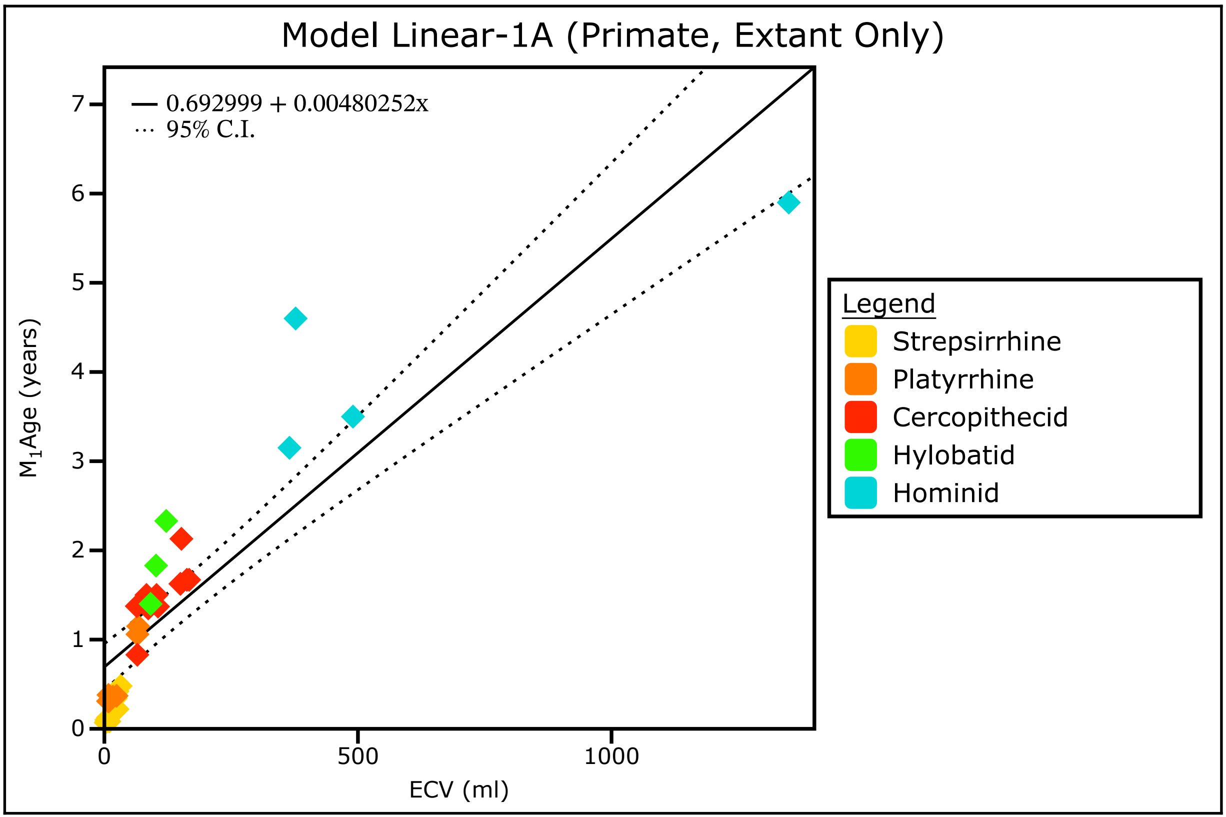

**FIGURE 5.3 REGRESSION PLOT: LINEAR-1A (PRIMATE, EXTANT ONLY)**

Model Linear-1A: Scatterplot for the extant primate sample (derived from 33 primate species; r = 0.88; $r^2$ = 0.77; p < 0.001; $s_e$ = 0.77).

Solid line represents least squares regression line, where y is $M_1$Age (years) and x is ECV (ml).

Dotted lines represent the upper and lower 95% confidence intervals.

Model Linear-1A predicts $M_1$Age as follows: *H. erectus* = 5.2 yr; *H. sapiens* = 7.2 yr; *P. troglodytes* = 2.5 yr.

Within the Linear Set 1 extant models, the coefficient of determination is greater in Model Linear-1C (Catarrhine). Within the Group-1A (Primate, Extant Only) models, the coefficient of determination in the third level polynomials is greater than in the $\ln$-transformed and Linear models

## Section 5.1.1.C Model Linear-1A (Primate, Extant Only)

Model Linear-1A (Primate, Extant Only) was created using a linear regression with the extant primate species data points (without ln-transformation). Model Linear-1A produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.692999 + 0.004803\ x$$

Model Linear-1A has a highly positive correlation ($r = 0.88$, $p < 0.001$, $s_e$=0.77). Model Linear-1A pred-$M_1$Ages are within RC for *H. sapiens* and *P. troglodytes* and over-predicted for *H. erectus* (*H. erectus* = 5.2 yr, *H. sapiens* = 7.2 yr, and *P. troglodytes* = 2.4 yr). Linear-1A pred-$M_1$Ages for the remaining fossil hominins are as follows: fossil *H. sapiens* = 7.8 yr ; *H. neanderthalensis* = 7.7 yr*;* and the Australopiths = 3.0 yr*.* Therefore, the predicted $M_1$Age for *P. troglodytes* is under-predicted, while both *H. erectus* and *H. sapiens* are over-predicted*.* Model Linear-1A does not meet the Stage 1 inclusion criteria.

Linear-1A *H*-residual = -1.277, and *P*-residual = 0.704. The *H. erectus Ha*-$M_1$Age = 3.9 yr, which is at the lower limit of RC, but not within AC. Applying the *H*a-$M_1$Ages for the other three fossil hominins are all outside of AC (above or below). *H. erectus P*a-$M_1$Age = 5.9 yr which is over-predicted outside RC. The *P*a-$M_1$Ages for the other three fossil hominins are all over-predicted outside RC. Model Linear-1A (Primate, Extant Only) does not meet the stage 1 criteria.

|  | **CUBIC-1A** | **ln-1A** | **"HUMAN-ADJUSTED" ln-1A** | **LINEAR-1A** | **"HUMAN-ADJUSTED" LINEAR-1A** |
|---|---|---|---|---|---|
| *H. erectus* | 3.9 | 7.1 | 4.5 | 5.2 | 3.9 |
| *P. troglodytes* | 3.5 | 3.5 | — | 2.4 | — |
| *H. sapiens* | 5.9 | 9.4 | — | 7.2 | — |
| Fossil *H. sapiens* | 7.7 | 10.2 | 6.3 | 7.8 | 6.5 |
| *H. neanderthalensis* | 7.1 | 10.0 | 6.2 | 7.6 | 6.3 |
| Australopiths | 3.8 | 4.3 | 2.7 | 3.0 | 1.7 |

**TABLE 5.1 GROUP 1A (PRIMATE, EXTANT ONLY): PREDICTED $M_1$AGE**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H. sapiens*-residual-adjusted values for the ln-transformed and linear models (cubic model *H. sapiens* residuals are too small to bring *H. erectus* into AC, so are not applied).

### Section 5.1.2 Group 1B (Haplorhine, Extant Only)

This section will now present the models built from Group 1B (Haplorhine, Extant Only). This is the group that excludes strepsirrhine data points. This is the same selection criteria as was used in Smith *et al.* (1995) and is important for determining if predictions perform well with only an update of data and no other changes. Only one of the Group 1B models passed the inclusion criteria for further discussion: the third degree polynomial model (Cubic-1B). Model $\ln$-1B (Haplorhine, Extant Only) and Model Linear-1B (Haplorhine, Extant Only) both only predict within RC after adjustment with the *H. sapiens*-residual. Note, again, that Model $\ln$-1B employs the same method and criteria as Smith *et al*. (Smith *et al.* 1995), so it is the starting point for analysing whether regression method predicts accurately with the updated $M_1$Age data.

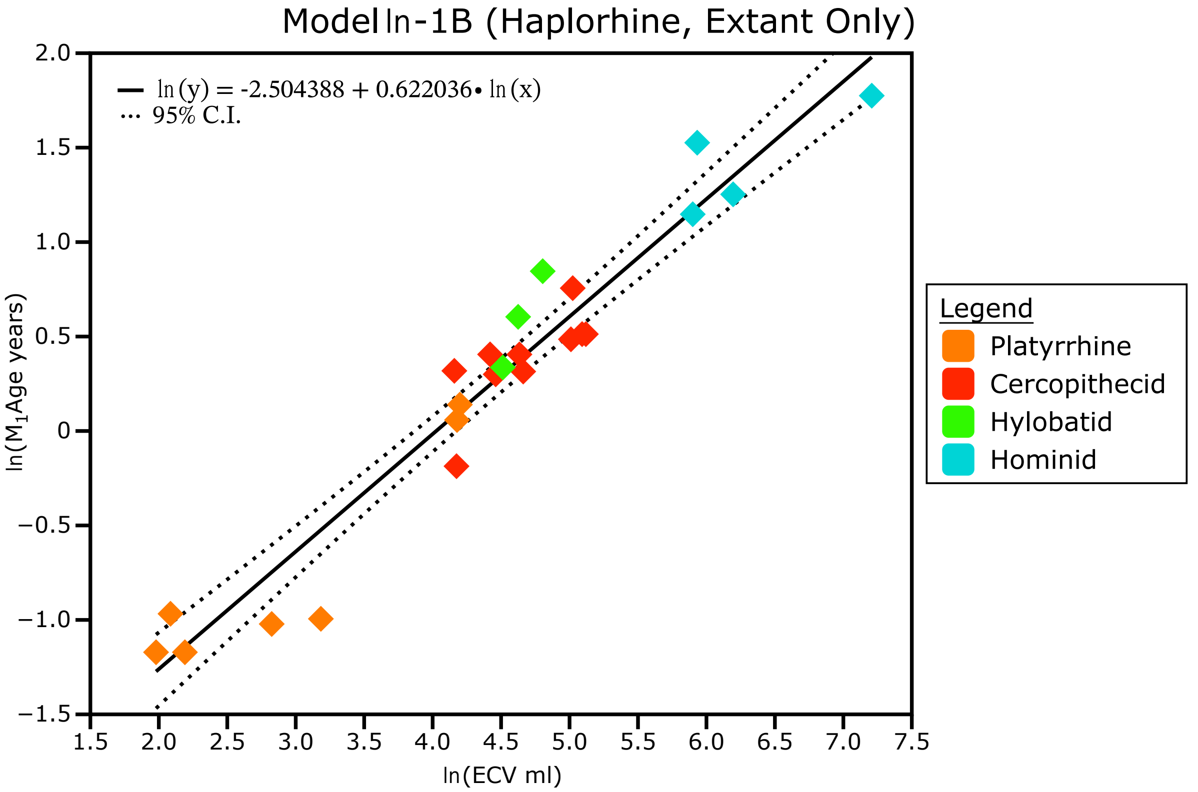

**FIGURE 5.4** **REGRESSION PLOT: ln-1B (HAPLORHINE, EXTANT ONLY)**

Model ln-1B: ln • ln scatterplot for the extant haplorhine sample (derived from 23 haplorhine species; $r = 0.99$, $r^2 = 0.98$, $p < 0.001$, $s_e$=0.210). Solid line represents the regression line, where y is $M_1$Age (years) and x is ECV (ml). Dotted lines represent the upper and lower 95% confidence intervals.

Model ln-1B predicts the three key hominids $M_1$Age as follows: *H. erectus* = 5.8 yr; *H. sapiens* = 7.2 yr; *P. troglodytes* = 3.2 yr.

Within the ln-transformed Set 1 (Extant Only) models, the coefficient of determination is greatest in this model. Within the Group-1B models, the coefficient of determination in the ln-transformed model is greater than in all the non-transformed models.

### Section 5.1.2.A Model $\ln$-1B (Haplorhine, Extant Only)

Model $\ln$-1B (Haplorhine, Extant Only) was created applying a linear regression to the two-sided $\ln$-transformed data using the extant haplorhine species. Model $\ln$-1B produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y) = -2.504388 + 0.622036 \ln(x)$$

Model $\ln$-1B has a very highly positive correlation (r=0.99, p<0.001, $s_e$=0.210). The pred-$M_1$Age is within AC for *P. troglodytes* (3.2 yr), and over-predicted outside RC for *H. sapiens* (7.2 yr) and *H. erectus* (5.8 yr). The pred-$M_1$Ages for the three remaining fossil hominins are all over-predicted above RC (fossil *H. sapiens* = 7.7 yr ; *H. neanderthalensis* = 7.6 yr; Australopiths = 3.8 yr). Model $\ln$-1B does not meet the stage 1 criteria (as defined in Section 4.2).

The $\ln$-1B *H*-residual = -0.204, and *P*-residual = -0.018. The *H*a-$M_1$Age for *H. erectus* = 4.7 yr, which is within AC. The *P*a-$M_1$Age is over-predicted outside RC for *H. erectus* (5.7 yr). The *H*a-$M_1$Age for the other fossil hominins are either within RC (Fossil *H. sapiens* = 6.3 yr; *H. neanderthalensis* = 6.2 yr; Australopiths = 3.1 yr), but only the Australopiths are also within AC. Applying the *P*-residual instead produces over-predicted *P*a-$M_1$Ages for all three of these fossil hominins. Model $\ln$-1B (Haplorhine, Extant Only) does not meet the stage 1 criteria.

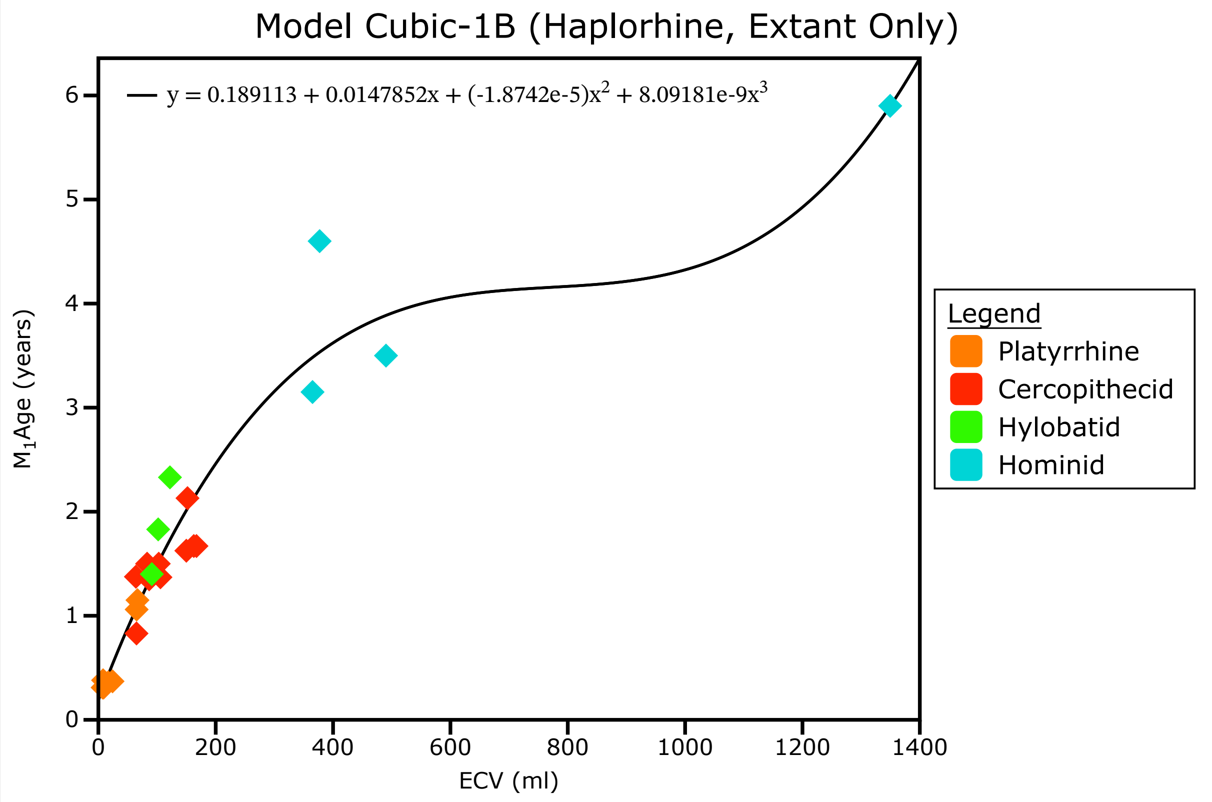

**Figure 5.5** **Regression Plot: Cubic-1B (Haplorhine, Extant Only)**

Model Cubic-1B (Haplorhine, Extant Only): scatterplot of the extant haplorhine sample (derived from 23 extant haplorhine species; $r = 0.97$, $r^2 = 0.94$, $p < 0.001$, $s_e = 0.372$). The line represents third level polynomial equation regression, where y is M$_1$Age (years) and x is endocranial volume (ml). Model Cubic-1B predicts M$_1$Age as follows: *H. erectus* = 4.2 yr; *H. sapiens* = 5.9 yr; *P. troglodytes* = 3.5 yr. Within the Cubic Set 1 models, the coefficient of determination is greatest in both Models Cubic-1A (Primate) and Cubic-1B (Haplorhine). Within the Group 1B models, the coefficient of determination in the $\ln$-transformed model is greater than in the non-transformed models.

## Section 5.1.2.B Model Cubic-1B (Haplorhine, Extant Only)

Model Cubic-1B (Haplorhine, Extant Only) was created using a third degree polynomial regression with the extant haplorhine species data points. Model Cubic-1B produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.189113 + 0.014785\, x - 0.00001874\, x^2 + 0.000000008092\, x^3$$

Model Cubic-1B has a very highly positive correlation ($r = 0.97$, $p < 0.001$, $s_e = 0.372$). The pred-$M_1$Ages for *H. erectus* (4.2 yr), *H. sapiens* (5.9 yr), and *P. troglodytes* (3.5 yr) are all within RC, and the former two are also within AC. Cubic-1B pred-$M_1$Ages for the other three fossil hominins are as follows: Fossil *H. sapiens* = 7.3 yr ; *H. neanderthalensis* = 6.9 yr*;* and the Australopiths = 3.9 yr*.* Therefore, the predicted $M_1$Age for *H. neanderthalensis* is within AC, while Fossil *H. sapiens* and the Australopiths are over-predicted above RC*.*

The Cubic-1B*,* the *H*-residual = −0.005*,* and the *P*-residual = −0.018. Due to the nature of the Cubic Models, the *H*-residuals are too small to impact *H. erectus* (which is already within AC), and the *P*-residuals reduce the prediction for *H. erectus* to below AC. Therefore residuals are not applied to adjust pred-$M_1$Ages for Model Cubic-1B. Model Cubic-1B (Haplorhine, Extant Only) meets the stage 1 criteria.

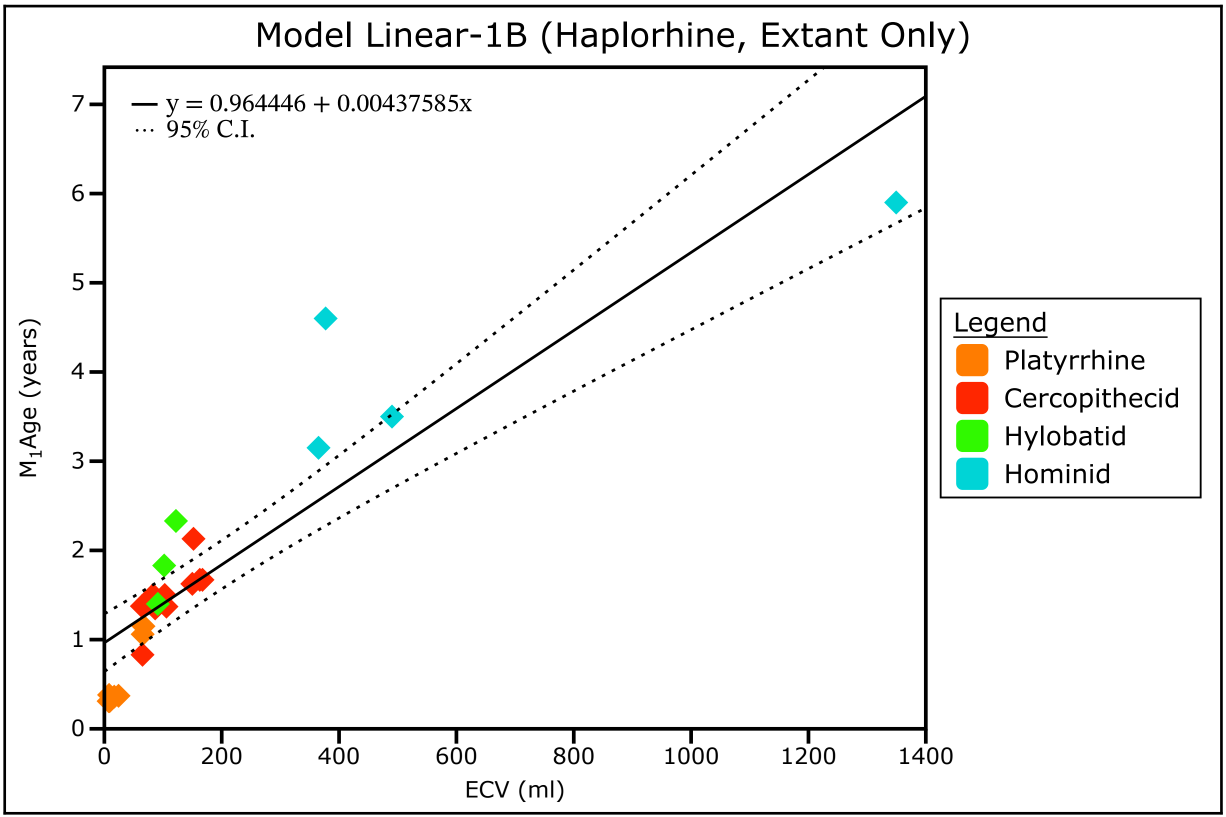

**Figure 5.6 Regression Plot: Linear-1B (Haplorhine, Extant Only)**
Model Linear-1B (Haplorhine, Extant Only): scatterplot for the extant Haplorhine sample (derived from 23 haplorhine species; r = 0.89, $r^2$ = 0.79, p < 0.001, $s_e$ = 0.642).
Main line represents the linear regression, where y is $M_1$Age (years) and x is endocranial volume (ml).
Dotted lines represent the upper and lower 95% confidence intervals.
Model Linear-1B predicts $M_1$Age as follows: *H. erectus* = 5.1 yr; *H. sapiens* = 6.9 yr; *P. troglodytes* = 2.6 yr.
Within the Linear Set 1 models, the coefficient of determination is greater in Model Linear-1C (Catarrhine). Within the Group-1B models, the coefficient of determination in the ln-transformed model is greater than in the non-transformed models.

## Section 5.1.2.C Model Linear-1B (Haplorhine, Extant Only)

Model Linear-1B (Haplorhine, Extant Only) was created using a linear regression with the extant haplorhine species data points (without ln-transformation). Model Linear-1B produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.964446 + 0.004376\,x$$

Model Linear-1B has a highly positive correlation (r=0.89, p<0.001, $s_e$=0.642). Model Linear-1B pred-$M_1$Ages are outside RC for *H. erectus* (5.1 yr) and for *H.*

*sapiens* (6.9 yr) and *P. troglodytes* (2.6 yr). Linear-1B pred-$M_1$Ages are over-predicted above RC for Fossil *H. sapiens* (7.5 yr) and *H. neanderthalensis* (7.3 yr); and predicted within AC for Australopiths (3.1 yr).

The Linear-1B *H*-residual = -0.972 and the *P*-residual = 0.588. *Ha*-$M_1$Age is within RC for *H. erectus* (4.1 yr). *Pa*-$M_1$Age is over-predicted outside of RC for *H. erectus* (5.6 yr). *Ha*-$M_1$Ages are predicted over RC for Fossil *H. sapiens* (6.5 yr), under AC for *H. neanderthalensis* (6.3 yr) and under RC for Australopiths (2.1 yr). *Pa*-$M_1$Ages are over-predicted above RC for Fossil *H. sapiens* (8.1 yr) and *H. neanderthalensis* (7.9 yr) the Australopiths (3.7 yr). Model Linear-1B (Haplorhine, Extant Only) does not meet the Stage 1 criteria for inclusion in Chapter 6, but the *H. erectus* predicted $M_1$Age does improve after adjustment with the Linear-1B residual. Table 5.3 presents the $M_1$Age prediction values of these three Group 1B (Haplorhine, Extant Only) models and the *H. sapiens* adjusted values for ln-1B and Linear-1B.

| | **Cubic-1B** | **ln-1B** | **"Human-adjusted" ln-1B** | **Linear-1B** | **"Human-adjusted" Linear-1B** |
|---|---|---|---|---|---|
| *H. erectus* | 4.2 | 5.8 | 4.7 | 5.1 | 4.1 |
| *P. troglodytes* | 3.5 | 3.2 | — | 2.6 | — |
| *H. sapiens* | 5.9 | 7.2 | — | 6.9 | — |
| Fossil *H. sapiens* | 7.3 | 7.7 | 6.1 | 7.5 | 6.5 |
| *H. neanderthalensis* | 6.8 | 7.5 | 6.1 | 7.3 | 6.3 |
| Australopiths | 3.8 | 3.8 | 3.1 | 3.1 | 2.6 |

**TABLE 5.2 GROUP 1B (HAPLORHINE, EXTANT ONLY): PREDICTED $M_1$AGE**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *Ha*-$M_1$Ages for the ln-transformed and linear models.

## Section 5.1.3 Group 1C (Catarrhine, Extant Only)

This section now presents the results for models using the extant Catarrhine data set (Group 1C). The models which predict *H. erectus* $M_1$Age within RC are: Cubic-1C and Linear 1C. Model ln-1C predicts *H. erectus* $M_1$Age outside RC. The following models predict *H. erectus* $M_1$Age within AC: Cubic-1C and Adjusted-Linear-1C. The presentation of Group 1C (Catarrhine, Extant Only) will begin with Model ln-1C (Catarrhine, Extant Only).

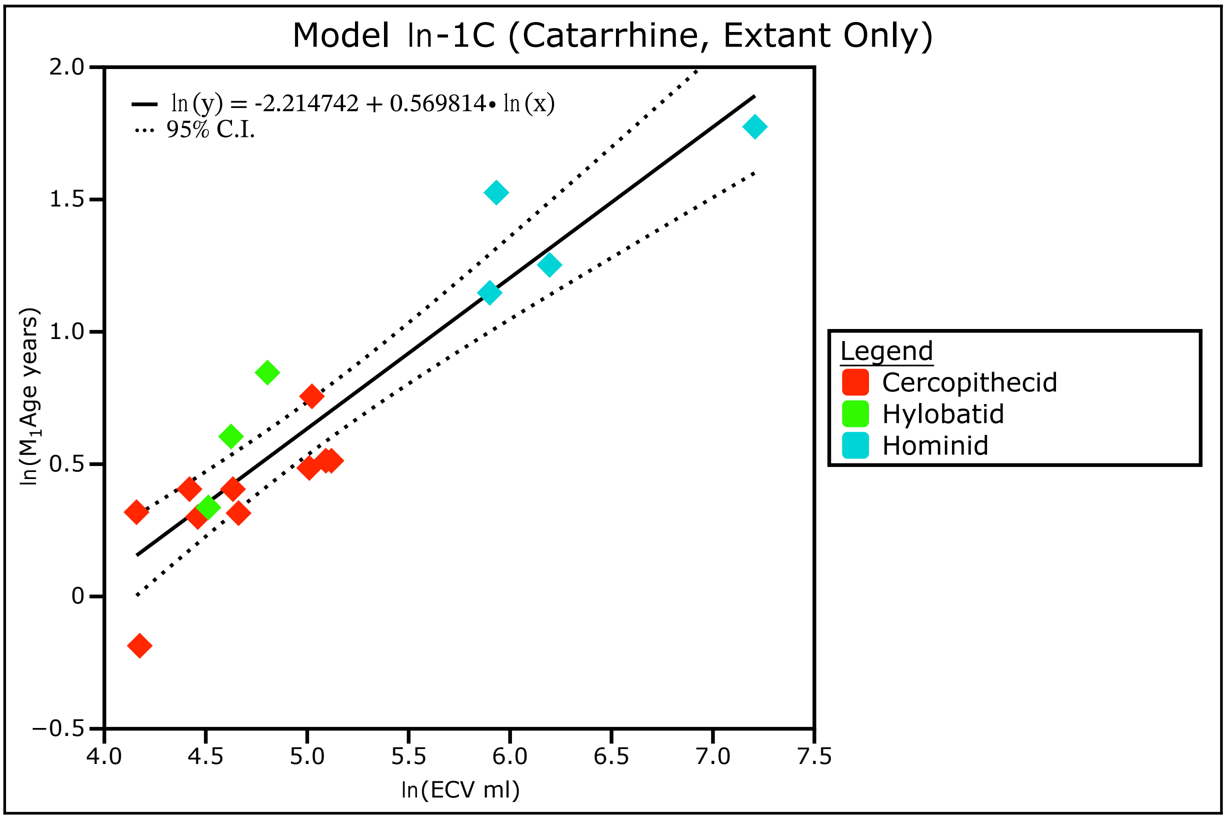

**FIGURE 5.7 REGRESSION PLOT: ln-1C (CATARRHINE, EXTANT ONLY)**

Model ln-1C: ln • ln scatterplot for the extant catarrhine sample (derived from 17 catarrhine species; r = 0.93, $r^2$ = 0.86, $p < 0.001$, $s_e$ = 0.194).
Solid line represents the regression line, where y is $M_1$Age (years) and x is ECV (ml).
Dotted lines represent the upper and lower 95% confidence intervals.
Model ln-1C predicts the three key hominids $M_1$Age as follows: *H. erectus* = 5.4 yr; *H. sapiens* = 6.6 yr; *P. troglodytes* = 3.1 yr.
Within the ln-transformed Set 1 (Extant Only) models, the coefficient of determination is greater in Model ln-1B (Haplorhine). Within the Group-1C (Catarrhine, Extant Only) models, the coefficient of determination in the second and third level polynomials is greater than in the ln-transformed and linear models.

### Section 5.1.3.A Model ln-1C (Catarrhine, Extant Only)

Model ln-1C (Catarrhine, Extant Only) was created applying a linear regression to the two-sided ln-transformed data using the extant catarrhine species. Model ln-1C produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y) = -2.214742 + 0.569814 \bullet \ln(x)$$

Model ln-1C has a very highly positive correlation ($r = 0.93$, $p < 0.001$, $s_e$=0.194). Model ln-1C pred-$M_1$Age is outside RC for *H. erectus* (5.4 yr) and *H. sapiens* (6.6 yr), and within AC for *P. troglodytes* (3.1 yr).. Model ln-1C pred-$M_1$Age is over RC for fossil *H. sapiens* (7.0 yr) and the Australopiths (3.7 yr), and within AC for *H. neanderthalensis* (6.9 yr).

The Model ln-1C *H*-residual = –0.117, and *P*-residual = 0.0003. The *H*a-$M_1$Age is within RC for *H. erectus* (4.8 yr). *P*a-$M_1$Age is above RC for *H. erectus* (5.5 yr). The *H*a-$M_1$Age is above AC for Fossil *H. sapiens* = 6.2 yr, at the lower limit of RC for *H. neanderthalensis* (6.2 yr) and within RC for Australopiths (3.3 yr). The *P*a-$M_1$Age for these hominins is over-predicted above RC for *H. sapiens* (7 yr) and the Australopiths (3.7 yr), and predicted within AC for *H. neanderthalensis* (6.9 yr). Model ln-1C does not meet the Stage 1 criteria (as defined in Section 4.2).

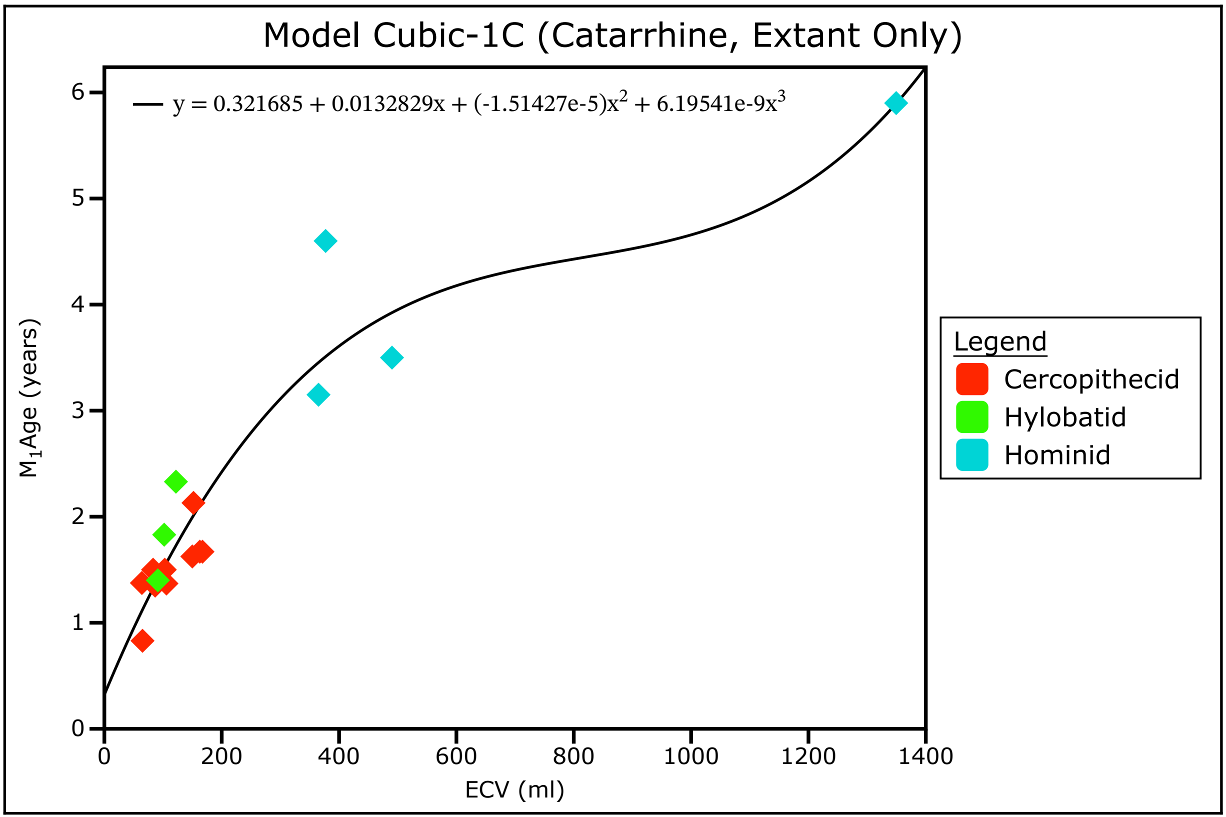

**FIGURE 5.8 REGRESSION PLOT: CUBIC-1C (CATARRHINE, EXTANT ONLY)**

Scatterplot for the extant catarrhine sample (derived from 17 extant catarrhine species; ($r$=0.95, $r^2$=0.90, $p<0.001$, $s_e$=0.457). The main line is a third level polynomial equation regression, where y is $M_1$Age (years) and x is endocranial volume (ml). Model Cubic-1C predicts $M_1$Age as follows: *H. erectus* = years; *H. sapiens* = years; *P. troglodytes* = 3.5 yr.

Within the Cubic Set 1 models, the coefficient of determination is greatest in both Models Cubic-1A (Primate) and Cubic-1B (Haplorhine). Within the Group-1C models, the coefficient of determination in the second and third level polynomials is greater than in the ln-transformed and linear models.

## Section 5.1.3.B Model Cubic-1C (Catarrhine, Extant Only)

Model Cubic-1C (Catarrhine, Extant Only) was created using a third degree polynomial regression with the extant catarrhine species data points. Model Cubic-1C (Catarrhine, Extant Only) produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.321685 + 0.013283x - 0.00001514x^2 + 0.000000006195x^3$$

Model Cubic-1C has a very highly positive correlation (R=0.95, p<0.001, $s_e$=0.457). Model Cubic-1C predicts $M_1$Age as follows: *H. erectus* $M_1$Age = 4.6 yr; *H. sapiens* = 5.9 yr; and *P. troglodytes* = 3.5 yr. Pred-$M_1$Age is over-predicted above RC for Fossil *H. sapiens*(7 yr) and Australopiths (3.9 yr), but predicted within AC for *H. neanderthalensis* (6.6 yr).

Model Cubic-1C *H*-residual = −0.003, and *P*-residual = −0.304. Due to the nature of the Cubic Models, the *H*-residuals are too small to bring predicted $M_1$Age for *H. erectus* into AC, and the *P*-residuals reduce the prediction for *H. erectus* to below AC. Therefore residuals are not applied with Model Cubic. Model Cubic-1C meets the stage 1 criteria (see Section 4.2).

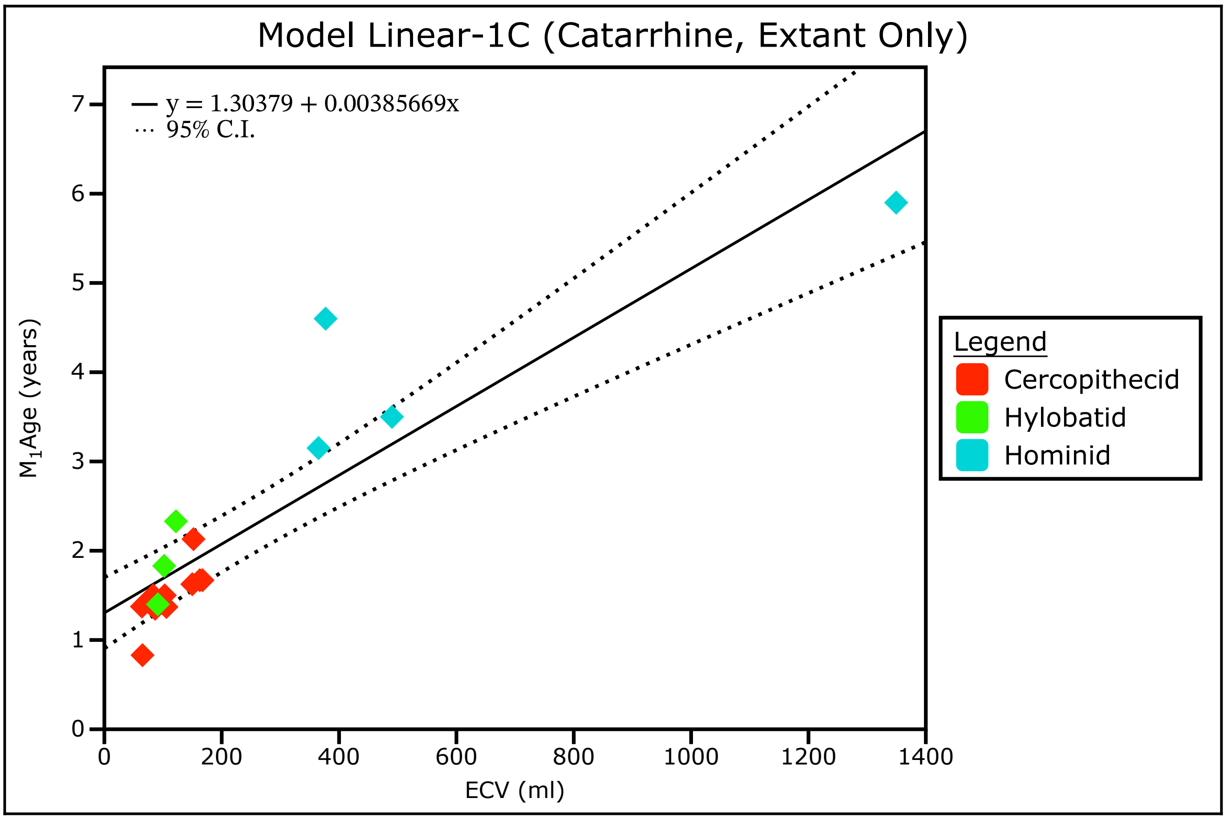

**FIGURE 5.9 REGRESSION PLOT: LINEAR-1C (CATARRHINE, EXTANT ONLY)**
Model Linear-1C: scatterplot for the extant catarrhine sample (derived from 17 catarrhine species; $r = 0.9$, $r^2 = 0.81$, $p < 0.001$, $s_e = 0.607$).
Solid line represents the regression line, where y is $M_1$Age (years) and x is endocranial volume (ml).
Dotted lines represent the upper and lower 95% confidence intervals.
Model Linear-1C predicts the three key hominids $M_1$Age as follows: *H. erectus* = 4.9 yr; *H. sapiens* = 6.5 yr; *P. troglodytes* = 2.7 yr.
Within the Linear Set 1 models, the coefficient of determination is greater in Model Linear-1C (Catarrhine). Within the Group-1C models, the coefficient of determination in the second level polynomial model (Cubic-1C) is greater than in the ln-1C and Linear-1C models.

## Section 5.1.3.C Model Linear-1C (Catarrhine, Extant Only)

Model Linear-1C (Catarrhine, Extant Only) was created using a linear regression with the extant catarrhine species data points (without ln-transformation). Model Linear-1C produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 1.303791 + 0.003857\,x$$

Model Linear-1C has a highly positive correlation ($r = 0.9$, $p < 0.001$, $s_e = 0.607$). Model Linear-1C pred-$M_1$Ages are just above RC for *H. erectus* (4.9

yr) and *H. sapiens* (6.5 yr), and within RC but below AC for *P. troglodytes* (2.7 yr). Linear-1C pred-$M_1$Age is over-predicted above RC for Fossil *H. sapiens* (7.0 yr) and predicted within AC for *H. neanderthalensis* (6.9 yr) and the Australopiths (3.2 yr).

The Model Linear-1C*, H*-residual = -0.611*,* and *P*-residual = 0.438. The *H*a-$M_1$Age for *H. erectus* is within AC (4.3 yr). *H*a-$M_1$Age is within RC but not AC for Fossil *H. sapiens* (6.4 yr) and *H. neanderthalensis* (6.3 yr), and below RC for the Australopiths (2.6 yr). The *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.3 yr). *P*a-$M_1$Age is over-predicted above RC for the three other fossil hominins (Fossil *H. sapiens* = 7.5 yr; *H. neanderthalensis* = 7.3 yr; Australopiths = 3.6 yr). Model Linear-1C (Catarrhine, Extant Only) meets the Stage 1 criteria for inclusion in Chapter 6.

| | **Cubic-1C** | **ln-1C** | **"adjusted" ln-1C** | **Linear -1C** | **"adjusted" Linear-1C** |
|---:|:---:|:---:|:---:|:---:|:---:|
| *H. erectus* | 4.6 | 5.4 | 4.8 | 4.9 | 4.3 |
| *H. sapiens* | 5.9 | 6.6 | — | 6.5 | — |
| *P. troglodytes* | 3.5 | 3.1 | — | 2.7 | — |
| Australopiths | 3.9 | 3.6 | 3.3 | 3.1 | 2.6 |
| Fossil *H. sapiens* | 7.0 | 7.0 | 6.2 | 6.9 | 6.4 |
| *H. neanderthalensis* | 6.6 | 6.9 | 6.1 | 6.7 | 6.3 |

**Table 5.3 Group 1C (Catarrhine, Extant Only): Predicted $M_1$Age**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H. sapiens*-residual-adjusted values for the ln-transformed and linear models.

## Section 5.2 Set 2 Models (Extant & Extinct)

The next sections now moves to the Set 2 (Extant and Extinct Species) models, which included extinct data points alongside the extinct data points. As explained in Data & Methods, for each group (2A-2E), four equation types were used to create four models each (see Section 4.2) only the linear model passed for 2B and 2C. This created twenty Set 2 (Extant & Extinct) models, which were subjected to the inclusion criteria outlined in Chapter 4. In the Set 2 models, level second level polynomial equations models ("Quad-2_" models) performed better than the third level polynomial models, so this section presents the ln-transformed, quadratic, and linear models.

Within the ln-transformed models, the only model which predicts *H. erectus* $M_1$Age within RC without adjustment with the *H. sapiens* residual is Model ln-2D (Hominoid, Extant & Extinct).

The detailed discussion of the successful models within Set 2 (Extant & Extinct) then follows, covering Group 2D Models (Hominoid, Extant & Extinct) and then Group 2E Models (Hominid, Extant & Extinct).

### Section 5.2.1 Group 2A (Primate, Extant & Extinct)

No Group 2A (Primate, Extant & Extinct) models predicts *H. erectus* $M_1$Age within RC without adjustment with the *H*-residual. The following Group 2A models predict *H.erectus* $M_1$Age only after adjustment with the *H. sapiens* residual: ln-2A and Linear-2A. Of the Group 2A models, only Adjusted-ln-2A predicts *H. erectus* $M_1$Age within AC.

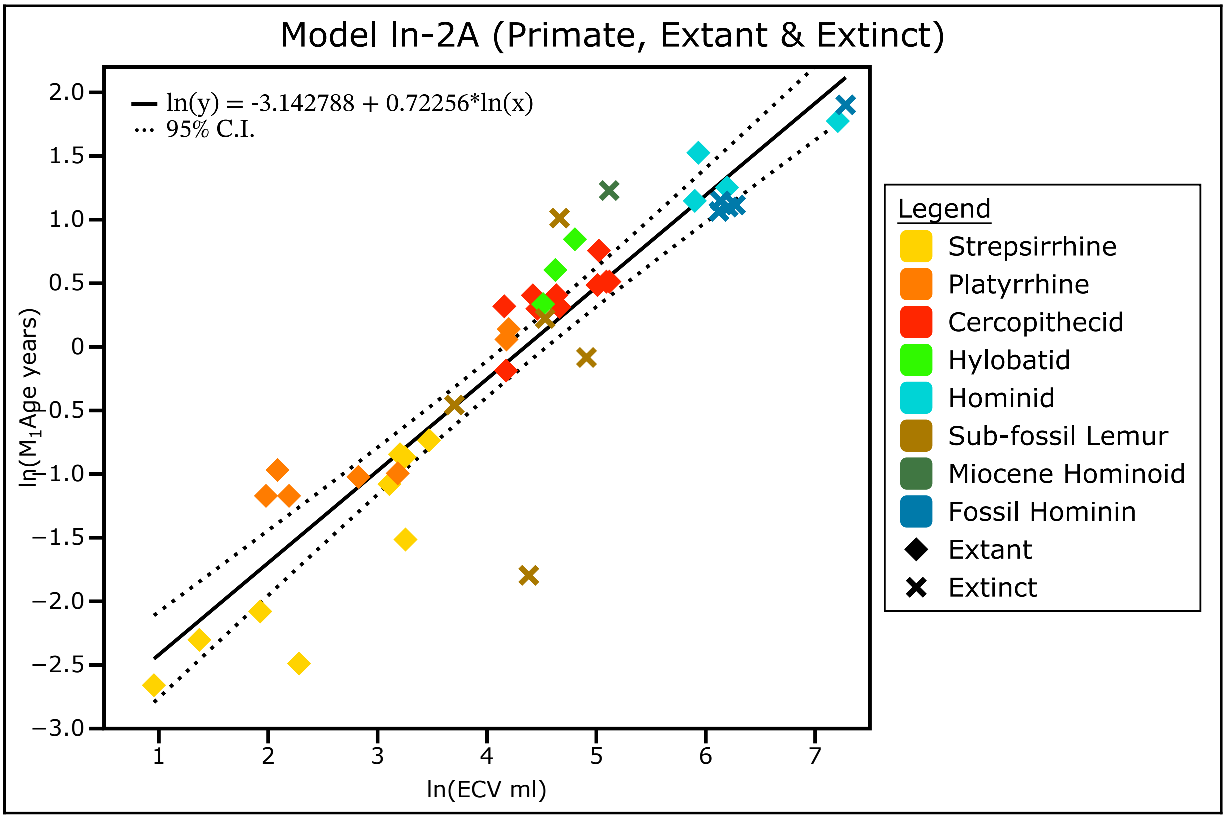

**Figure 5.10 Regression Plot: ln-2A (Primate, Extant & Extinct)**

Model ln-2A (Primate,Extant & Extinct): two sided ln-transformed scatterplot for the extant & extinct primate sample (derived from 44 primate species; $r = 0.92$, $r^2 = 0.85$, $p < 0.001$, $s_e = 0.459$).

Solid line represents the regression line, where y is $M_1$Age (years) and x is ECV (ml).

Dotted lines represent the upper and lower 95% confidence intervals.

Model ln-2A predicts the three key hominids $M_1$Age as follows: *H. erectus* = 6 yr; *H. sapiens* = 7.9 yr; *P. troglodytes* = 3.1 yr.

Within the ln-transformed Set 2 (Extant & Extinct models), the coefficient of determination is greater in Model ln-2B (Haplorhine, Extant & Extinct). Within the Group-2A models, the coefficient of determination in the third level polynomial model is greater than in all other models.

## Section 5.2.1.A Model ln-2A (Primate, Extant & Extinct)

Model ln-2A (Primate, Extant & Extinct) was created applying a linear regression to the two-sided ln-transformed data using the extant & extinct primate species. Model ln-2A produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y) = -3.142788 + 0.722560 \bullet \ln(x)$$

Model ln-2A has a very highly positive correlation ($r = 0.92$, $p < 0.001$, $s_e = 0.459$). Model ln-2A pred$M_1$Age is over-predicted above RC for *H. erectus* (6 yr) and *H. sapiens* (7.9 yr), but predicted within AC for *P. troglodytes* (3.1 yr). Model ln-2A pred-$M_1$Age is over-predicted for fossil *H. sapiens* (8.5 yr)*, H. neanderthalensis* (8.3 yr)*,* and the Australopiths (3.8 yr)*.*

The Model ln-2A *H*-residual = -0.290*,* and the *P*-residual = 0.027. *H*a-$M_1$Age predicts within AC for *H. erectus* (4.5 yr). *H*a-$M_1$Age is predicted within RC for Fossil *H. sapiens* (6.3 yr) and *H. neanderthalensis* (6.2 yr), and within AC for the Australopiths (2.8 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (6.2 yr). *P*a-$M_1$Age is overpredicted above RC for the other fossil hominins (fossil *H. sapiens* = 8.7 yr, *H. neanderthalensis* = 8.5 yr, Australopiths = 3.9 yr). Model ln-2A (Primate, Extant & Extinct) does not meet the stage 1 criteria.

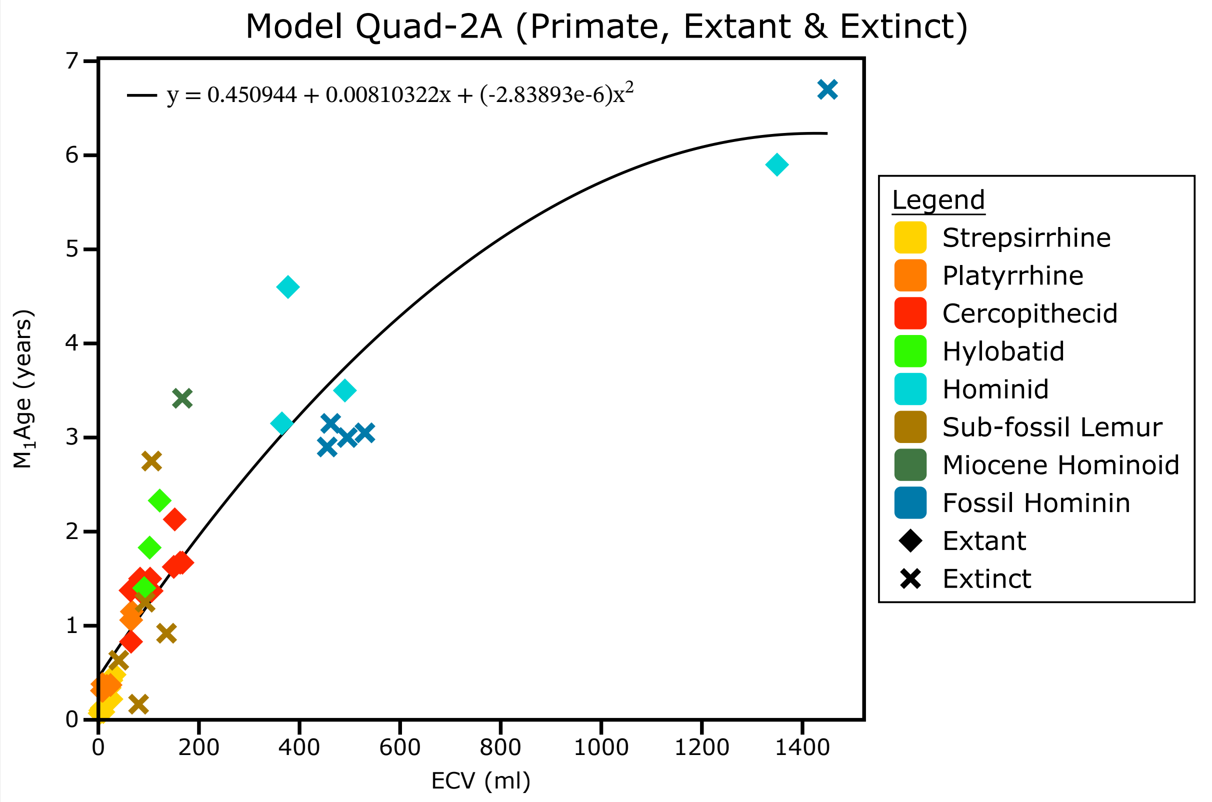

**Figure 5.11 Regression Plot: Quad-2A (Primate, Extant & Extinct)**

Model Quad-2A: scatterplot for the extant & extinct Primate sample (derived from 44 Primate species) ($r = 0.93$, $r^2 = 0.86$, $p < 0.001$, $s_e = 0.77$).

Solid line represents the second level polynomial equation regression line, where y is M1Age (years) and x is endocranial volume (ml).

Model Quad-2A predicts M1Age as follows: H. erectus = 5.6 yr; H. sapiens = 6.2 yr; P. troglodytes = 3 yr.

Within the Quad Set 2 models, the coefficient of determination is greater in Model Quad-2B (Haplorhine). Within the Group-2A models, the coefficient of determination in the third level polynomial model is greater than in other models.

## Section 5.2.1.B Model Quad-2A (Primate, Extant & Extinct)

Model Quad-2A (Primate, Extant & Extinct) was created using a second degree polynomial regression with the extant & extinct primate species data points. Model Quad-2A produced the following equation (where y is M1Age in years and x is ECV in ml):

$$y = 0.450944 + 0.008103x - 0.000002839\,x^2$$

Model Quad-2A has a very highly positive correlation ($r = 0.93$, $p < 0.001$, $s_e = 0.77$). Model Quad-2A pred-$M_1$Age is over-predicted above RC for *H. erectus* (5.6 yr), within RC for *H. sapiens* (6.2 yr), and within AC for *P. troglodytes* (3 yr). Pred-$M_1$Age is predicted within RC for Fossil *H. sapiens* (6.2 yr) and *H. neanderthalensis* (6.2 yr), and above RC for the Australopiths (3.7 yr).

Model Quad-2A *H*-residual = -0.316, and *P-r*esidual = 0.1197. *H*a-$M_1$Age over-predicts above RC for *H. erectus* (5.2 yr). *H*a-$M_1$Age predicts within AC for Fossil *H. sapiens* (5.9 yr), within RC for the Australopiths (3.4 yr), and under-predicts below RC for *H. neanderthalensis* (5.9 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.7 yr). *P*a-$M_1$Age predicts within RC for *H. sapiens* (6.3 yr) and *H. neanderthalensis* (6.4 yr), and over-predicts above RC for the Australopiths (3.8 yr). Model Quad-2A (Primate, Extant & Extinct) does not meet the stage 1 criteria (see Section 4.2).

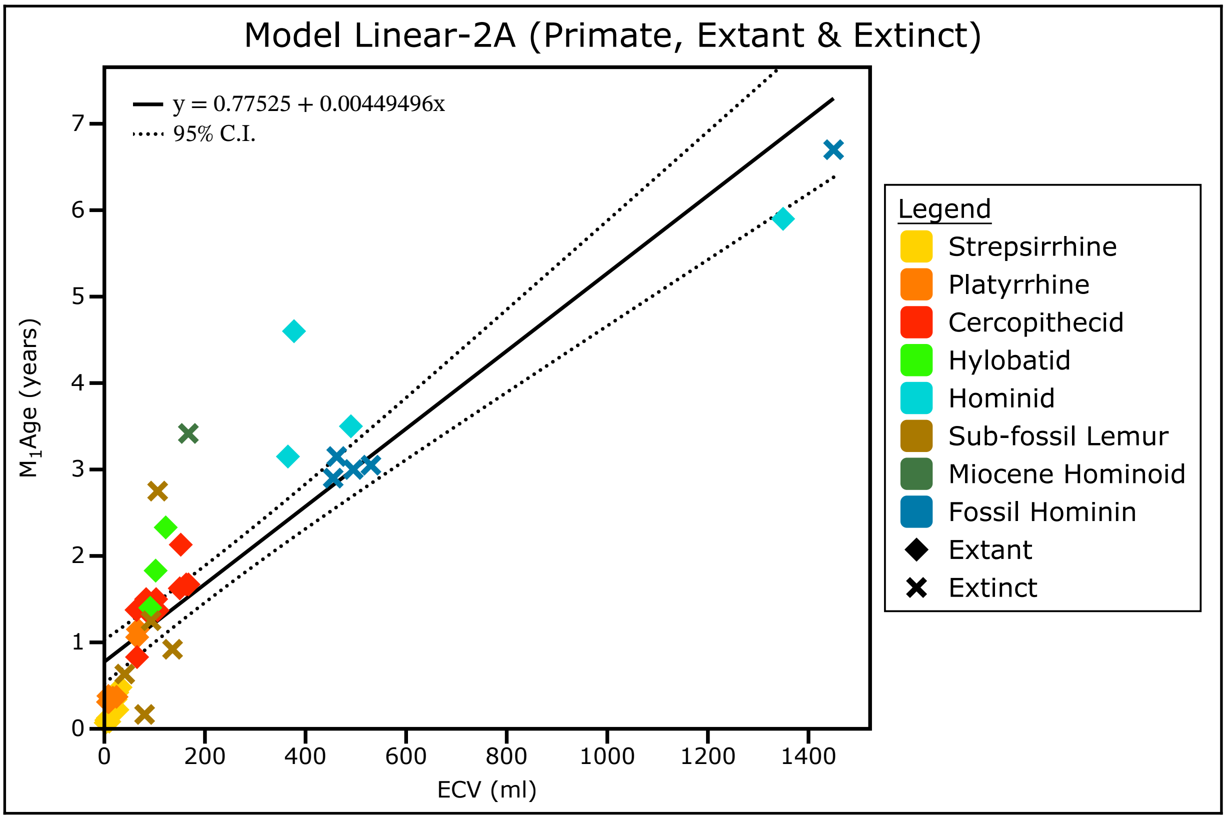

**FIGURE 5.12 REGRESSION PLOT: LINEAR-2A (PRIMATE, EXTANT & EXTINCT)**
Scatterplot for the extant & extinct primate sample (derived from 44 primate species; $r = 0.89$; $r^2 = 0.79$; $p < 0.001$; $s_e = 0.70$). Solid line represents least squares regression line, where y is $M_1$Age (years) and x is ECV (ml). The dotted lines represent the upper and lower 95% confidence intervals.
Model Linear-2A predicts the three key hominids' $M_1$Age as follows: *H. erectus* = 5 yr; *H. sapiens* = 6.8 yr; *P. troglodytes* = 2.4 yr.
Within the Linear Set 2 (Extant & Extinct) models, the coefficient of determination is greater in Model Linear-2C (Catarrhine, Extant & Extinct).
Within the Group-2A (Primate, Extant & Extinct) models, the coefficient of determination in the second level polynomial model (Quad-2A) is greater than in this and the $\ln$-2A model.

## Section 5.2.1.C Model Linear-2A

Model Linear-2A (Primate, Extant & Extinct) was created using a linear regression with the extant & extinct primate species data points (without $\ln$-transformation). Model Linear-2A produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.77525 + 0.004495\,x$$

Linear-2A has a highly positive correlation ($r = 0.89$, $p < 0.001$, $s_e = 0.70$).

Model Linear-2A pred-$M_1$Age is over-predicted above RC for *H. erectus* (5 yr), *H.*

*sapiens (*6.8 yr), and is under-predicted below RC for *P. troglodytes* = *(*2.4 yr). Pred-$M_1$Age is within AC for Australopiths (3.0 yr) and is overpredicted above RC for Fossil *H. sapiens* (7.5 yr) and *H. neanderthalensis* (7.3 yr).

The Linear-2A *H*-residual = -0.944 and the *P*-residual = 0.734. *H*a-$M_1$Age is predicted within RC for *H. erectus* (4 yr). *H*a-$M_1$Age is over-predicted above RC for Fossil *H. sapiens* (6.5 yr), is predicted within RC but below AC for *H. neanderthalensis* (6.3 yr), and is predicted below RC for the Australopiths (2.0 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.7 yr). *Pa*-$M_1$Age is predicted outside of AC for the other 3 fossil hominins. Model Linear-2A (Primate, Extant & Extinct) does not meet the stage 1 criteria. A comparison table of Group-2A pred-$M_1$Ages is included below.

| | **ln-2A** | ***H*-ADJUSTED ln-2A** | **QUAD-2A** | ***H*-ADJUSTED QUAD-2A** | **LINEAR-2A** | ***H*-ADJUSTED LINEAR-2A** |
|---|---|---|---|---|---|---|
| *H. sapiens* | 7.9 | — | 6.2 | — | 6.8 | — |
| *P. troglodytes* | 3.1 | — | 3.9 | — | 2.4 | — |
| *H. erectus* | 6.0 | 4.5 | 5.6 | 5.2 | 5.0 | 4.0 |
| Australopiths | 3.7 | 2.8 | 3.7 | 3.4 | 2.9 | 2.0 |
| Fossil *H. sapiens* | 8.5 | 6.3 | 6.2 | 5.9 | 7.5 | 6.5 |
| *H. neanderthalensis* | 8.3 | 6.2 | 6.2 | 5.9 | 7.3 | 6.3 |

**TABLE 5.4 GROUP 2A (PRIMATE, EXTANT & EXTINCT): PREDICTED $M_1$AGE**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H. sapiens*-residual-adjusted values for each.

## Section 5.2.2 Models, Group 2B (Haplorhine, Extant & Extinct)

This section presents three Group 2B (Haplorhine, Extant & Extinct) models: ln-2B, Quad-2B, and Linear-2B. Each model is presented by sub-sections which begin with the plotted regression on the even page followed by the sub-section heading and text.

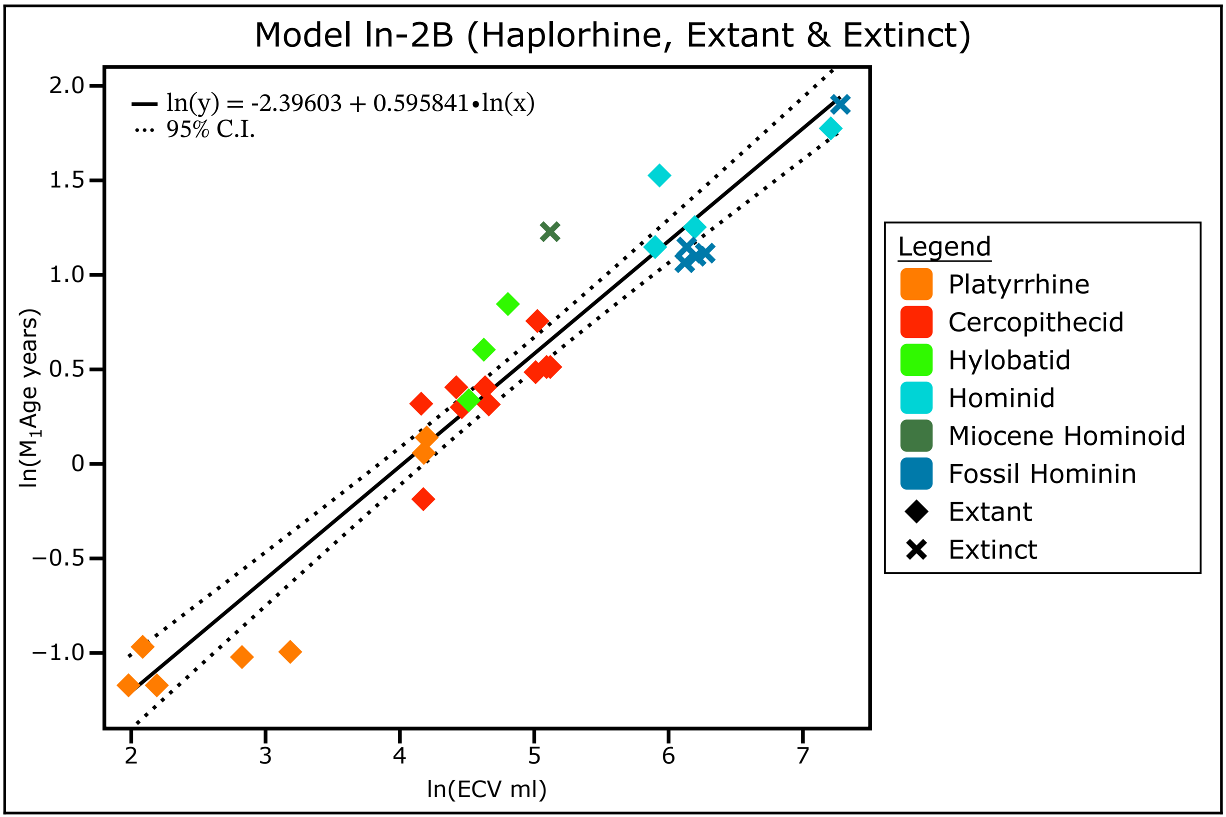

**Figure 5.13 Regression Plot: ln-2B (Haplorhine, Extant & Extinct)**
ln•ln scatterplot for the extant & extinct haplorhine sample (derived from 30 haplorhine species; $r=0.96$, $r^2=0.92$, $pp<0.001$, $s_e=0.229$). Solid line represents the regression line, where y is $M_1$Age (years) and x is ECV (ml). Dotted lines represent the upper and lower 95% confidence intervals.
Model ln-2B predicts the three key hominids $M_1$Age as follows: *H. erectus* = 5.4 yr; *H. sapiens* = 6.7 yr; *P. troglodytes* = 3.1 yr.
Within the ln-transformed Set 2 extant & extinct models, the coefficient of determination is greater in Model ln-2B (Haplorhine). Within the Group-2B models, the coefficient of determination in the ln-transformed (ln-2B) and in the second level polynomial (Quad-2B) models are greater than in the Linear-2B model.

## Section 5.2.2.A Model ln-2B (Haplorhine, Extant & Extinct)

Model ln-2B (Haplorhine, Extant & Extinct) was created applying a linear regression to the two-sided ln-transformed data using the extant & extinct haplorhine species. Model ln-2B produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y) = -2.396030 + 0.595841 \bullet \ln(x)$$

Model ln-2B has a very highly positive correlation (r = 0.96, r2 = , $p < 0.001$, $s_e = 0.229$). Model ln-2B pred-$M_1$Age is over-predicted above RC for *H. erectus* (5.4 yr) and *H. sapiens (*6.7 yr), and is predicted within AC for *P. troglodytes* (3.1 yr). The Model ln-2B pred-$M_1$Age is predicted above RC for Fossil *H. sapiens* (7.1 yr) and Australopiths (3.6 yr), and within RC but above AC for *H. neanderthalensis* (7.0 yr).

The Model ln-2B *H*-residual = -0.124*,* and *P*-residual = 0.028. *H*a-$M_1$Age predicts within RC for *H. erectus* (4.7 yr) which is closer to the observed *H. erectus* $M_1$Age. *H*a-$M_1$Age is predicted within RC for Fossil *H. sapiens* (6.2 yr) and *H. neanderthalensis* (6.2 yr), and within AC for the Australopiths (3.2 yr). *P*a-$M_1$Age over-predicts above RC for *H. erectus* (5.5 yr). *P*a-$M_1$Age is over predicted above RC for Fossil *H. sapiens* (7.3 yr) and Australopiths (3.7 yr), and is predicted within RC but above AC for *H. neanderthalensis* (7.2 yr). Model ln-2B (Haplorhine, Extant & Extinct) does not meet the stage one criteria (see Section 4.2.4)

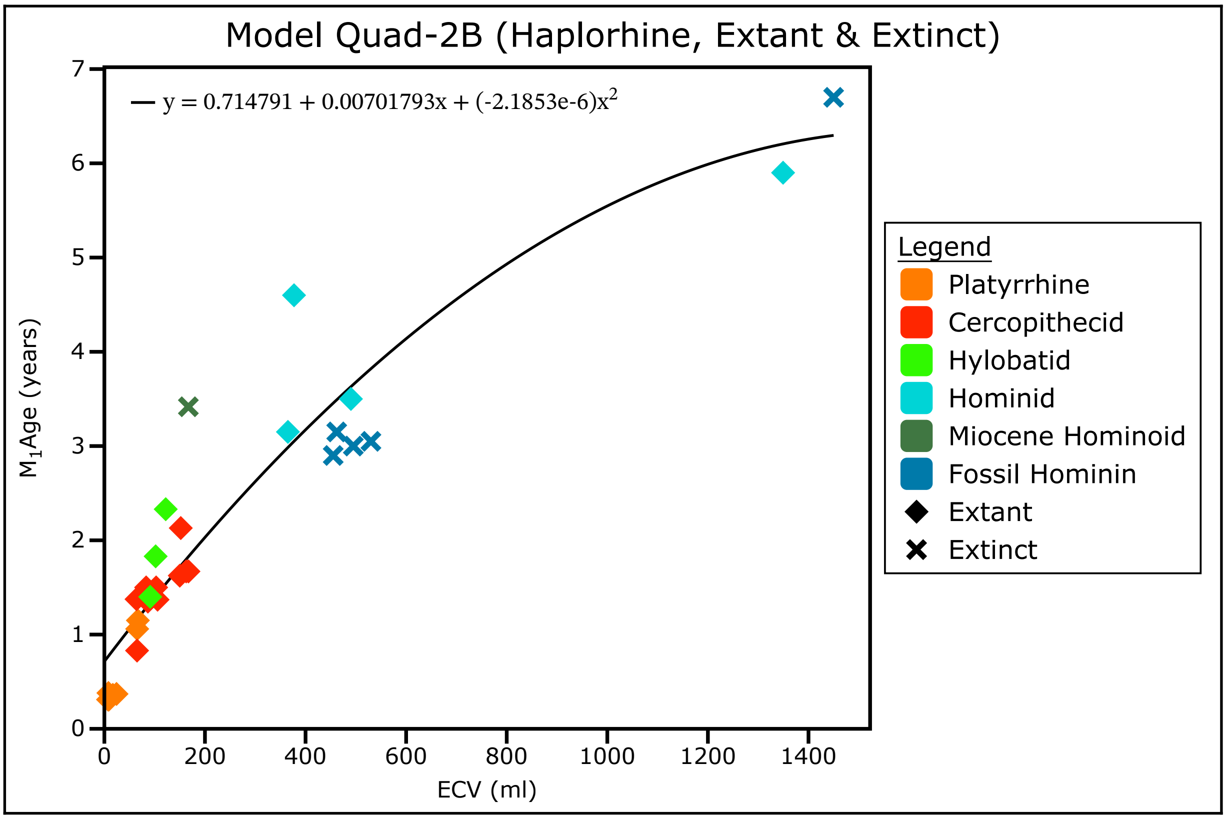

**FIGURE 5.14 REGRESSION PLOT: QUAD-2B (HAPLORHINE, EXTANT & EXTINCT)**

Model Quad-2B (Haplorhine, Extant & Extinct): scatterplot regression for the extant haplorhine sample (derived from 23 haplorhine species; $r = 0.94$, $r^2 = 0.92$, $p < 0.001$, $s_e = 0.396$).

This model does not meet criteria range, before or after adjustment.

Main line represents the second level polynomial equation regression line, where y is $M_1$Age (years) and x is endocranial volume (ml).

Model Quad-1B predicts $M_1$Age as follows: *H. erectus* = 5.9 yr; *H. sapiens* = 5.9 yr; *P. troglodytes* = 3.5 yr.

Within the Quad Set 2 (Extant & Extinct) models, the coefficient of determination is greater in Model Quad-1A (Primate). Within the Group-2B models, the coefficient of determination in ln-2B and Quad-2B is greater than the Linear-2B models.

## Section 5.2.2.B Model Quad-2B (Haplorhine, Extant & Extinct)

Model Quad-1B (Haplorhine, Extant Only) was created using a second degree polynomial regression with the extant haplorhine species data points. Model Quad-1B produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 0.432038 + 0.010071\,x - 0.000004488\,x^2$$

Model Quad-1B has a very highly positive correlation (R=0.96, p<0.001, $s_e$**=**0.396). Model Quad-1B pred-$M_1$Age is above RC for *H. erectus* (5.4 yr), is within AC for *H. sapiens* (5.9 yr) and within RC for *P. troglodytes* (3.5 yr). Pred-$M_1$Age is within RC for Fossil *H. sapiens* predicted (5.5 yr), is under-predicted below RC for *H. neanderthalensis* (5.6 yr), and is over-predicted above RC for Australopiths (4.3 yr).

The Quad-1B *H*-residual = 0.052 and *P*-residual = -0.360. *H*a-$M_1$Age is over-predicted above RC for *H. erectus* (6 yr). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (5.5 yr), and is over-predicted above RC for *H. neanderthalensis* (5.7 yr) and Australopiths (4.3 years). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.6 yr). *P*a-$M_1$Age is under-predicted below RC for Fossil *H. sapiens* (5.1 years) and *H. neanderthalensis* (5.2 yr), and is over-predicted above RC for Australopiths (3.9 yr). Model Quad-1B (Haplorhine, Extant Only) does not meet the stage 1 criteria.

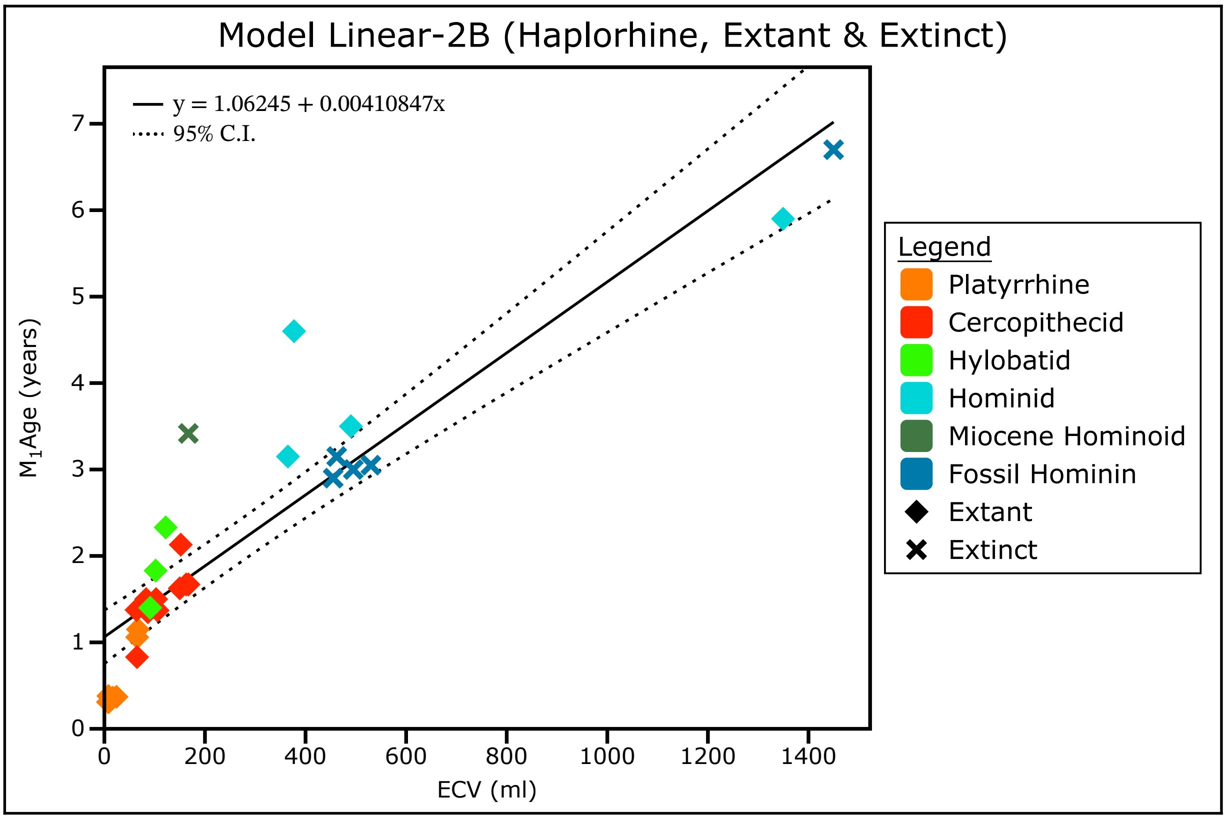

**Figure 5.15 Regression Plot: Linear-2B (Haplorhine, Extant & Extinct)**

Model Linear-2B (Haplorhine, Extant & Extinct): scatterplot for the extant & extinct haplorhine sample (derived from 30 haplorhine species; r = R value; $r^2$=0.83; p<0.001; $s_e$=0.661). Solid line represents least squares regression line, where y is $M_1$Age (years) and x is ECV (ml). The dotted lines represent the upper and lower 95% confidence intervals. Model Linear-2B predicts $M_1$Age as follows: *H. erectus* = 4.9 yr; *H. sapiens* = 6.6 yr; *P. troglodytes* = 2.6 yr.

Within the Linear Set 2 extant & extinct models, the coefficient of determination is greater in Model Linear-2C (Catarrhine).

Within the Group-2B (Haplorhine, Extant & Extinct) models, the coefficient of determination in the $\ln$-transformed ($\ln$-2A) and in the second level polynomial (Quad-2A) models are greater than in the Linear-2B model.

## Section 5.2.2.C Model Linear-2B (Haplorhine, Extant & Extinct)

Model Linear-2B (Haplorhine, Extant & Extinct) was created using a linear regression with the extant & extinct haplorhine species data points (without $\ln$-transformation). Model Linear-2B produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 1.062449 + 0.004108\,x$$

Model Linear-2B has a very highly positive correlation (r = 0.91, $r^2$= 0.83, p < 0.001, $s_e$=0.661). Pred-$M_1$Age is predicted within RC for *H. erectus* (4.9 yr), and predicted outside RC for *H. sapiens* (6.6 yr) and *P. troglodytes* (2.6 yr). Pred-$M_1$Age is predicted within AC for Australopiths (3.1 yr), is over-predicted above RC for Fossil *H. sapiens* (7.2 yr), and is within RC for *H. neanderthalensis* (7.0 yr).

The Model Linear-2B *H-r*esidual = -0.708 and *P*-residual = 0.588. *H*a-$M_1$Age is predicted within AC for *H. erectus* (4.2 yr). *H*a-$M_1$Age is over-predicted above RC for Fossil *H. sapiens* (6.5 yr), is within RC for *H. neanderthalensis* (6.3yr), and is under-predicted below RC for Australopiths (2.3 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.5 yr). *P*a-$M_1$Age is over-predicted above RC for Fossil *H. sapiens* (7.8 yr), *H. neanderthalensis* (7.6 yr), and the Australopiths (3.6 yr). Model Linear-2B (Haplorhine, Extant & Extinct) meets stage one criteria, and improves with adjustment with the *H*-residual. A comparison table of predicted $M_1$Ages from Group 2B (Haplorhine, Extant & Extinct) is provided below.

| | **ln-2B** | ***H*-adjusted ln-2B** | **Quad-2B** | ***H*-adjusted Quad-2B** | **Linear-2B** | ***H*-adjusted Linear-2B** |
|---|---|---|---|---|---|---|
| *H. erectus* | 6.0 | 4.5 | 5.4 | 5.1 | 5.0 | 4.0 |
| *H. sapiens* | 7.9 | — | 6.2 | — | 6.8 | — |
| *P. troglodytes* | 3.1 | — | 3.0 | — | 2.4 | — |
| Australopiths | 3.7 | 2.8 | 3.6 | 3.3 | 2.9 | 2.0 |
| Fossil *H. sapiens* | 8.5 | 6.3 | 6.2 | 6.0 | 7.5 | 6.5 |
| *H. neanderthalensis* | 8.3 | 6.2 | 6.2 | 6.0 | 7.3 | 6.3 |

**Table 5.5 Group 2B (Haplorhine, Extant & Extinct): Predicted $M_1$Age**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H. sapiens*-residual-adjusted values for each.

## Section 5.2.3 Models, Group 2C (Catarrhine, Extant & Extinct)

In Group 2C (Catarrhine, Extant & Extinct), only Model Linear-2C met the inclusion criteria (see Chapter 4). Models ln-2C and Quad-2C met inclusion range for *H. erectus* after adjustment with the *H. sapiens*-residual. Cubic models were not a good fit for any of the Set 2 (Extant & Extinct) models. The presentation of Group 2C (Catarrhine, Extant & Extinct) will begin with Model ln-2C.

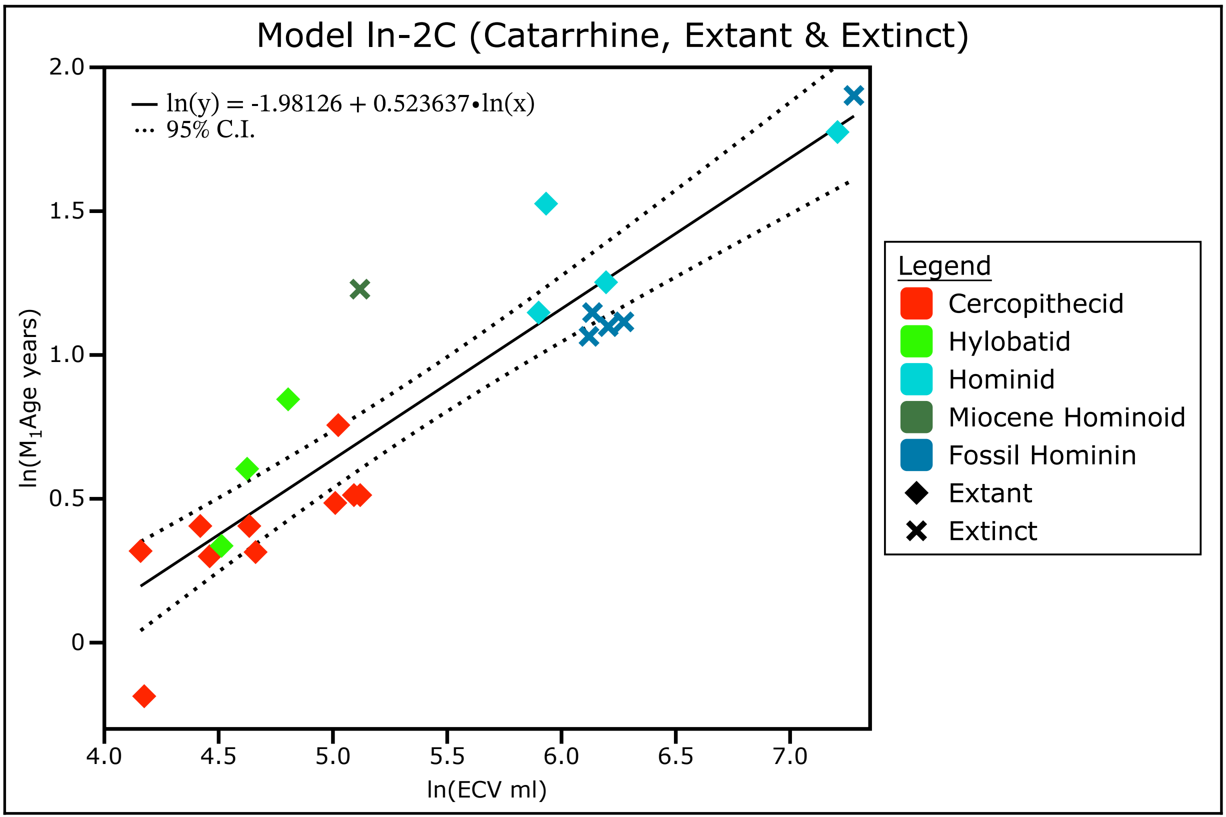

**FIGURE 5.16 REGRESSION PLOT: ln-2C (CATARRHINE, EXTANT & EXTINCT)**
Model ln-2C (Catarrhine, Extant & Extinct): two-sided ln-transformed scatterplot linear regression of the extant & extinct catarrhine sample (derived from 23 catarrhine species; $r = 0.92$, $r^2 = 0.85$, $p < 0.001$, $s_e = 0.215$).
Solid line represents the linear regression line, where y is $M_1$Age (years) and x is ECV (ml). Dotted lines represent the upper and lower 95% confidence intervals. Model ln-2C predicts the three key hominids $M_1$Age as follows: *H. erectus* = 5 yr; *H. sapiens* = 6 yr; *P. troglodytes* = 3 yr. Within the ln-transformed Set 2 extant & extinct models, the coefficient of determination is greater in Model ln-2B (Haplorhine). Within the Group-2C (Catarrhine, Extant & Extinct) models, the coefficient of determination is greater in the second level polynomial (Quad-2C) than in the other two models. However, they are all nearly equal (0.86 vs 0.85 in the other two).

## Section 5.2.3.A Model ln-2C (Catarrhine, Extant & Extinct)

Model ln-2C (Catarrhine, Extant & Extinct) was created applying a linear regression to the two-sided ln-transformed data using the extant & extinct primate species. Model ln-2A produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y)= 0.5236\bullet\ln(x) - 1.9812$$

Model ln-2C (Catarrhine, Extant & Extinct) has a very highly positive correlation ($r = 0.92$; $p < 0.001$; $s_e = 0.215$). Pred-$M_1$Age is over-predicted above RC for *H. erectus* (5 yr), and is within AC for *H. sapiens* (6 yr) and *P. troglodytes* (3 yr). Pred-$M_1$Age is predicted within RC for Fossil *H. sapiens* (6.3 yr), *H. neanderthalensis* (6.2 yr) and Australopiths (3.5 yr).

Model ln-2C *H*-residual = -0.018 and *P*-residual = 0.039. *H*a-$M_1$Age is predicted within RC for *H. erectus* (4.9 yr). *H*a-$M_1$Age is predicted within RC for Fossil *H. sapiens* (6.1 yr) and Australopiths (3.5 yr), and is under-predicted below RC for *H. neanderthalensis* (6.1 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.2 yr). *P*a-$M_1$Age is over-predicted above RC for Fossil *H. sapiens* (6.6 yr) and the Australopiths (3.7 yr), and is within AC for *H. neanderthalensis*. Model ln-2C (Catarrhine, Extant & Extinct) does not meet stage one criteria.

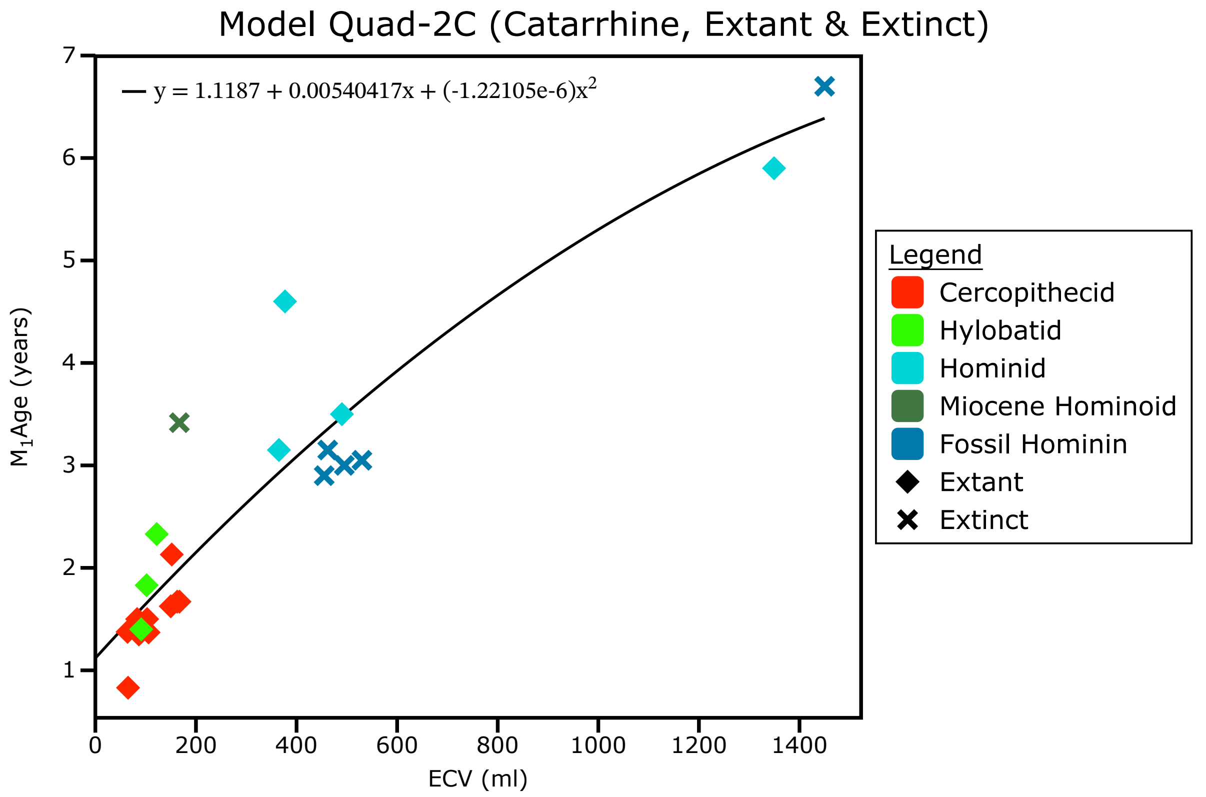

**FIGURE 5.17 REGRESSION PLOT: QUAD-2C (CATARRHINE, EXTANT & EXTINCT)**

Model Quad-2C (Catarrhine, Extant & Extinct): scatterplot for the extant & extinct catarrhine sample (derived from 23 catarrhine species; $r = 0.93$, $r^2 = 0.86$, $p < 0.001$, $s_e = 0.607$).

Main line represents second level polynomial (quadratic) regression line, where y is $M_1$Age (years) and x is endocranial volume (ml).

Model Quad-2C predicts $M_1$Age as follows: *H. erectus* = 5.1 yr; *H. sapiens* = 6.2 yr; *P. troglodytes* = 2.9 yr.

Within the Quad Set 2 models, the coefficient of determination is greater in Model Quad-2B (Haplorhine). Within the Group-2C (Catarrhine, Extant & Extinct) models, the coefficient of determination is greater in the second level polynomial (Quad-2C) than in the other two models. However, they are all nearly equal (0.86 vs 0.85 in the other two).

## Section 5.2.3.B Model Quad-2C (Catarrhine, Extant & Extinct)

Model Quad-2C (Catarrhine, Extant & Extinct) was created using a second degree polynomial regression with the extant & extinct catarrhine species data points. Model Quad-2C produced the following equation (where y is M1Age in years and x is ECV in ml):

$$y = 1.118704 + 0.005404\,x - 0.000001221\,x^2$$

Model Quad-2C has a very highly positive correlation (r = 0.93, $p<0.001$, $s_e$ **=** 0.607). Model Quad-2C pred-$M_1$Age is over-predicted above RC for *H. erectus* (5.1 yr), and is within RC for *H. sapiens* (6.2yr) and *P. troglodytes* (2.9 yr). Pred-$M_1$Age is over-predicted above RC for Fossil *H. sapiens* (6.5 yr), and is within RC for *H. neanderthalensis* (6.4yr) and the Australopiths (3.5 yr).

The Model Quad-2C *H*-residual = -0.289 and *P*-residual = 0.222. *H*a-$M_1$Age is within RC for *H. erectus* (4.8yr). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.2 yr) and the Australopiths (3.2 yr), and is under-predicted below RC for *H. neanderthalensis* (6.1 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.3yr). *P*a-$M_1$Age is within AC for *H. neanderthalensis* (6.6 yr), and is overpredicted above RC for Fossil *H. sapiens* (6.7 yr) and the Australopiths (3.7 yr). Model Quad-2C (Catarrhine, Extant & Extinct) does not meet the Stage 1 criteria for inclusion in Chapter 6.

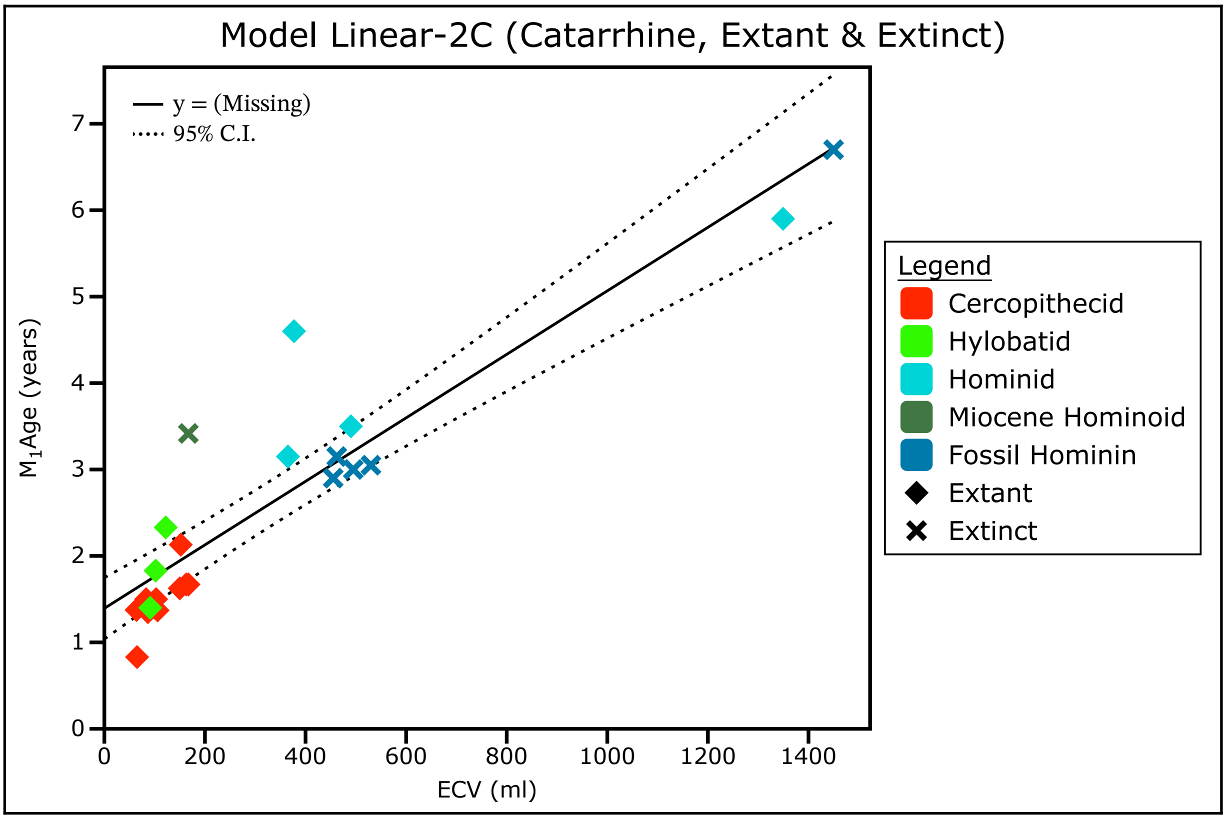

**FIGURE 5.18 REGRESSION PLOT: LINEAR-2C (CATARRHINE, EXTANT & EXTINCT)**
Model Linear-2C (Catarrhine, Extant & Extinct): scatterplot for the extant & extinct catarrhine sample (derived from 23 catarrhine species; r = R value; r2=0.85; p<0.001; $s_e$=0.608). Solid line represents least squares regression line, where y is M1Age (years) and x is ECV (ml). The dotted lines represent the upper and lower 95% confidence intervals.
Model Linear-2C predicts $M_1$Age as follows: *H. erectus* = 4.8 yr; *H. sapiens* = 6.4 yr; *P. troglodytes* = 2.7 yr.
Within the Set 2 (Extant & Extinct) Linear models, the coefficient of determination is greater in Model Linear-2C (Catarrhine).
Within the Group-2C (Catarrhine, Extant & Extinct) models, the coefficient of determination in the third level polynomials is greater than in all other models.

### Section 5.2.3.C Model Linear-2C (Catarrhine, Extant & Extinct)

Model Linear-2C (Catarrhine, Extant & Extinct) was created using a linear regression with the extant & extinct catarrhine species data points. Model Linear-2C produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 1.393364 + 0.003673\,x$$

Model Linear-2C has a very highly positive correlation (r=0.92, p<0.001, $s_e$=0.608). Model Linear-2C pred-$M_1$Age is witin RC for *H. erectus* (4.9 yr), *H.*

*sapiens* (6.4 yr), and *P. troglodytes (*2.7 yr). Pred-$M_1$Age is predicted within AC for *H. neanderthalensis* (6.7 yr) and the Australopiths (3.2 yr), and above RC for Fossil *H. sapiens* (6.9 yr).

The Model Linear-2C *H*-residual = -0.452 and *P*-residual = 0.416. *H*a-$M_1$Age is within AC for *H. erectus* (4.4 yr). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.4 yr), *H. neanderthalensis* (6.3 yr), and the Australopiths (2.7 yr). *P*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.2 yr). *P*a-$M_1$Age is within RC for *H. neanderthalensis* (7.1 yr) and is over-predicted above RC for Fossil *H. sapiens* (7.3yr) and Australopiths (3.6yr). Model Linear-2C (Catarrhine, Extant & Extinct) meets RC without adjustments. Below is a comparison table of pred-$M_1$Ages from the Group-2C models.

| | **ln-2C** | ***H*-adjusted ln-2C** | **Quad-2C** | ***H*-adjusted Quad-2C** | **Linear-2C** | ***H*-adjusted Linear-2C** |
|---|---|---|---|---|---|---|
| *H. erectus* | 5.0 | 4.9 | 5.1 | 4.8 | 4.8 | 4.4 |
| *H. sapiens* | 6.0 | — | 6.2 | — | 6.4 | — |
| *P. troglodytes* | 3.0 | — | 2.9 | — | 2.7 | — |
| Australopiths | 3.5 | 3.5 | 3.4 | 3.2 | 3.1 | 2.7 |
| *H. neanderthalensis* | 6.2 | 6.1 | 6.4 | 6.1 | 6.7 | 6.3 |
| Fossil *H. sapiens* | 6.5 | 6.2 | 6.5 | 6.2 | 6.9 | 6.4 |

**Table 5.6 Group 2C (Catarrhine, Extant & Extinct): Predicted $M_1$Age**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H. sapiens*-residual-adjusted values for each.

## Section 5.2.4 Models, Group 2D (Hominoid, Extant & Extinct)

This section presents three Group 2D (Hominoid, Extant & Extinct) Model results: ln-2D; Quad-2D, and Linear-2D. These are presented in sub-sections which begin on an even page with the associated figure plot for the model, followed by the sub-section heading in text.

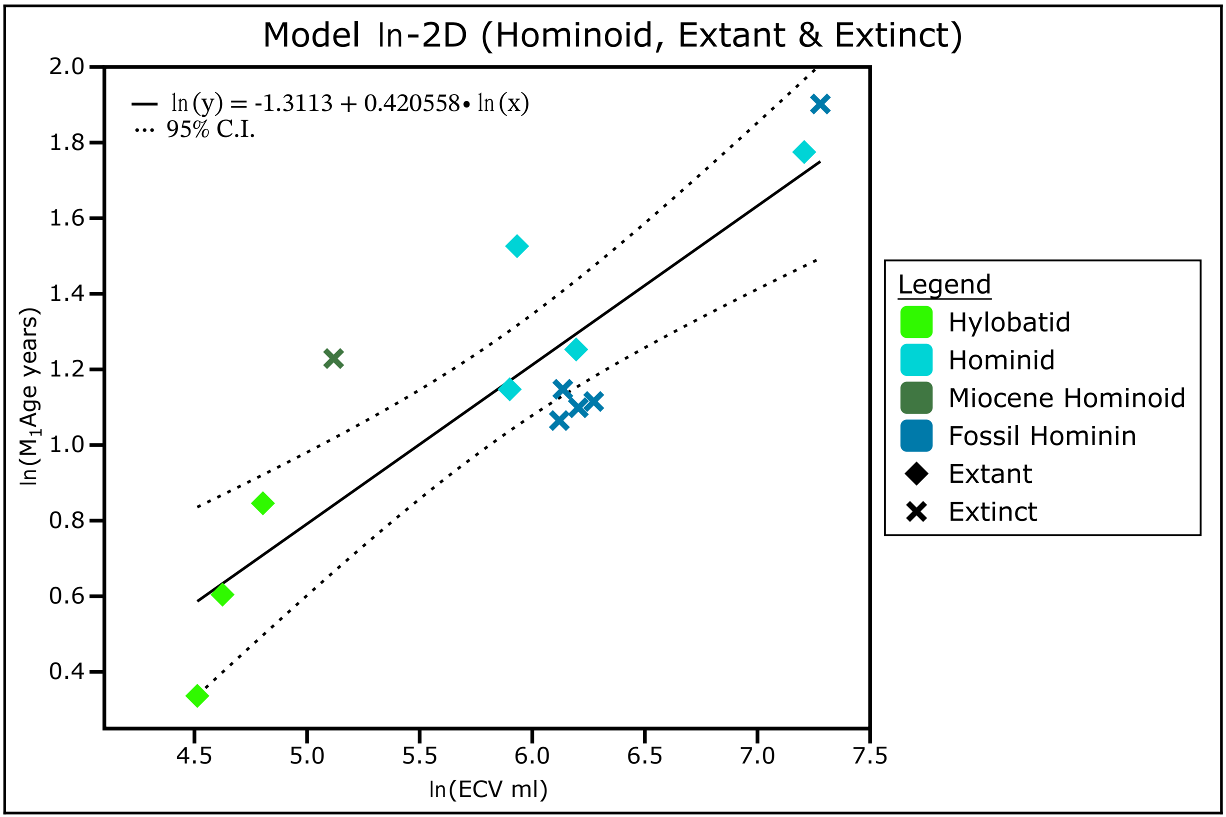

**Figure 5.19 Regression Plot: ln-2D (Hominoid, Extant & Extinct)**
Model ln-2D (Hominoid, Extant & Extinct): ln • ln scatterplot for the extant & extinct hominoid sample (derived from 13 hominoid species, $r^2 = 0.76$, $p < 0.001$, $s_e = 0.217$). Main line is a least squares regression, where y is $M_1$Age (years) and x is endocranial volume (ml), $\ln(y) = -1.311297 + 0.420558 \bullet \ln(x)$,. Dotted lines are the upper and lower 95% confidence intervals. Within the ln-transformed Set 2 models, the coefficient of determination is greater in Model ln-2B (Haplorhine). Within the Group-2D models, the coefficient of determination in the third level polynomials is greater than in all other models. Model ln-2D predicts $M_1$Age as follows: *H. erectus* = 4.8 yr; *H. sapiens* = 5.6 yr; *P. troglodytes* = 3.2 yr.

## Section 5.2.4.A Model ln-2D (Hominoid, Extant & Extinct)

Model ln-2D (Hominoid, Extant & Extinct) was created applying a linear regression to the two-sided ln-transformed data using the extant & extinct hominoid species. Model ln-2D produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$\ln(y) = -1.311297 + 0.420558 \bullet \ln(x)$$

Model ln-2D (Hominoid, Extant & Extinct) has a highly positive correlation ($r = 0.87$, $p < 0.001$, $s_e = 0.217$). Model ln-2D pred-$M_1$Age is within RC for *H. erectus* (4.8yr) and *H. sapiens* (5.6yr), and is within AC for *P. troglodytes* (3.2yr). Pred-$M_1$Age is within AC for Fossil *H. sapiens* (5.8 yr), and is outside RC for *H. neanderthalensis* (5.8 yr) and the Australopiths (3.6 yr).

The Model ln-2D *H*-residual = 0.055 and *P*-residual = -0.023. *H*a-$M_1$Age is over-predicted above RC for *H. erectus* (5.1 yr). *H*a-$M_1$Age is predicted within AC for Fossil *H. sapiens* (6.1yr), and is outside RC for *H. neanderthalensis* (6.1 yr) and the Australopiths (3.8 yr). *P*a-$M_1$Age is within RC for *H. erectus* (4.7 yr). *P*a-$M_1$Age is within AC for Fossil *H. sapiens* (5.7 yr), but is outside RC for *H. neanderthalensis* (5.6 yr) and the Australopiths (3.6 yr). Model ln-2D (Hominoid, Extant & Extinct) meets the stage 1 criteria.

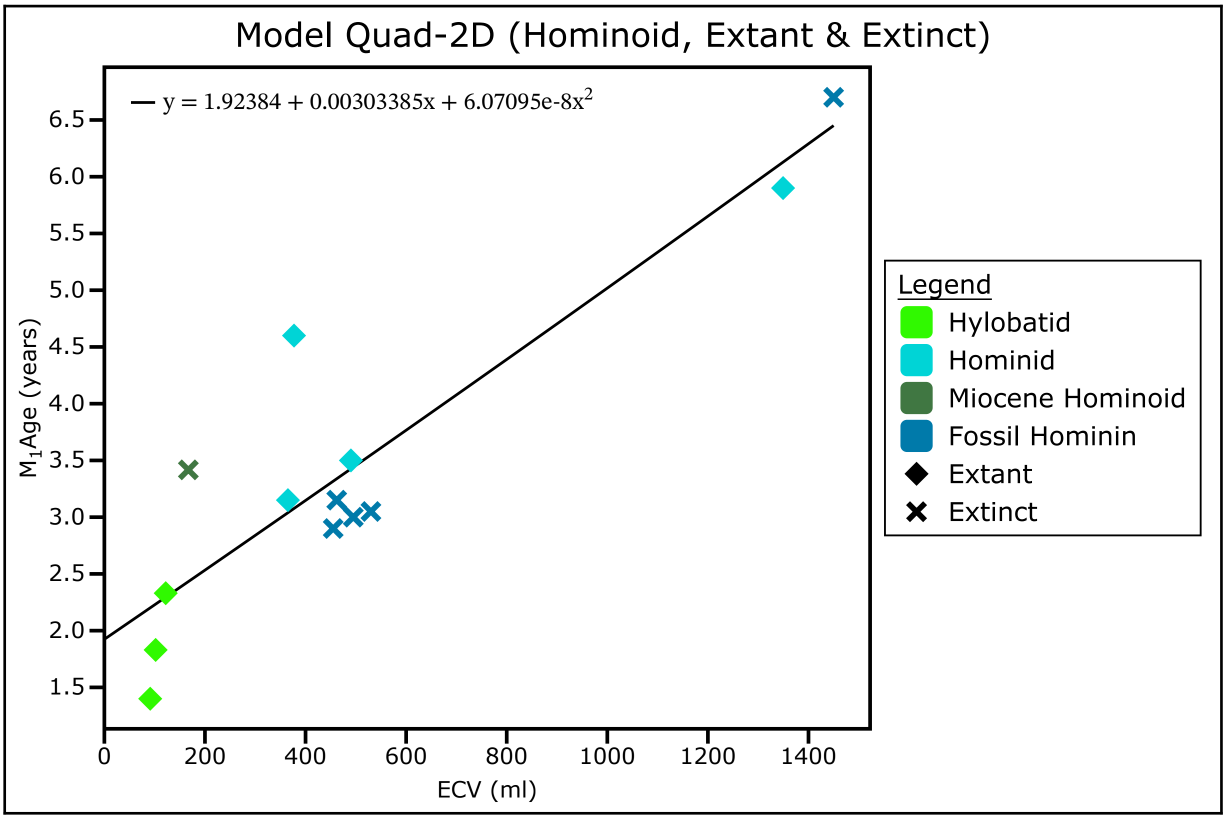

**FIGURE 5.20 REGRESSION PLOT: QUAD-2D (HOMINOID, EXTANT & EXTINCT)**

Model Quad-2D (Hominoid, Extant & Extinct): scatterplot for the extant & extinct hominoid sample (derived from 13 hominoid species, r = 0.90, $r^2$ = 0.81, $p < 0.001$, $s_e$ = 0.79). The solid line represents the second level polynomial equation regression line, where y is $M_1$Age (years) and x is ECV (ml).

Dotted lines represent the upper and lower 95% confidence intervals.

Model Quad-2D predicts $M_1$Age as follows: *H. erectus* = 4.7 yr; *H. sapiens* = 5.9 yr; *P. troglodytes* = 3 yr.

Within the Quad Set 2 models, the coefficient of determination is greater in Model Quad-2B (Haplorhine). Within the Group-2D models, the coefficient of determination in the third level polynomials is greater than in all other models. Model Quad-2D (Hominoid, Extant & Extinct)

## Section 5.2.4.B Model Quad-2D (Hominoid, Extant & Extinct)

Model Quad-2D (Hominoid, Extant & Extinct) was created using a second degree polynomial regression with the extant & extinct hominoid species data points. Model Quad-2D produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 1.923839 + 0.003034\,x - 0.00000006071\,x^2$$

Model Quad-2D has a very highly positive correlation (r=0.90, $p < 0.001$, $s_e$ = 0.79). Model Quad-2D pred-$M_1$Age within RC for *H. erectus* (4.7 yr), *H. sapiens* (5.9 yr), and *P. troglodytes* (3 yr). Pred-$M_1$Age is within RC for Fossil *H. sapiens* (6.3 yr), *H. neanderthalensis* (6.2 yr), and Australopiths (3.4 yr).

The Model Quad-2D *H*-residual = -0.009, and *P*-residual = 0.127. *H*a-$M_1$Age is within RC for *H. erectus* (4.7 yr). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.3 yr), *H. neanderthalensis* (6.2 yr), and the Australopiths = 3.4 yr.

*P*a-$M_1$Age is within RC for *H. erectus* (4.8 yr). *P*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.4 yr), *H. neanderthalensis* (6.3 yr) and the Australopiths (3.5 yr). Model Quad-2D (Hominoid, Extant & Extinct) meets the Stage 1 criteria without adjustment.

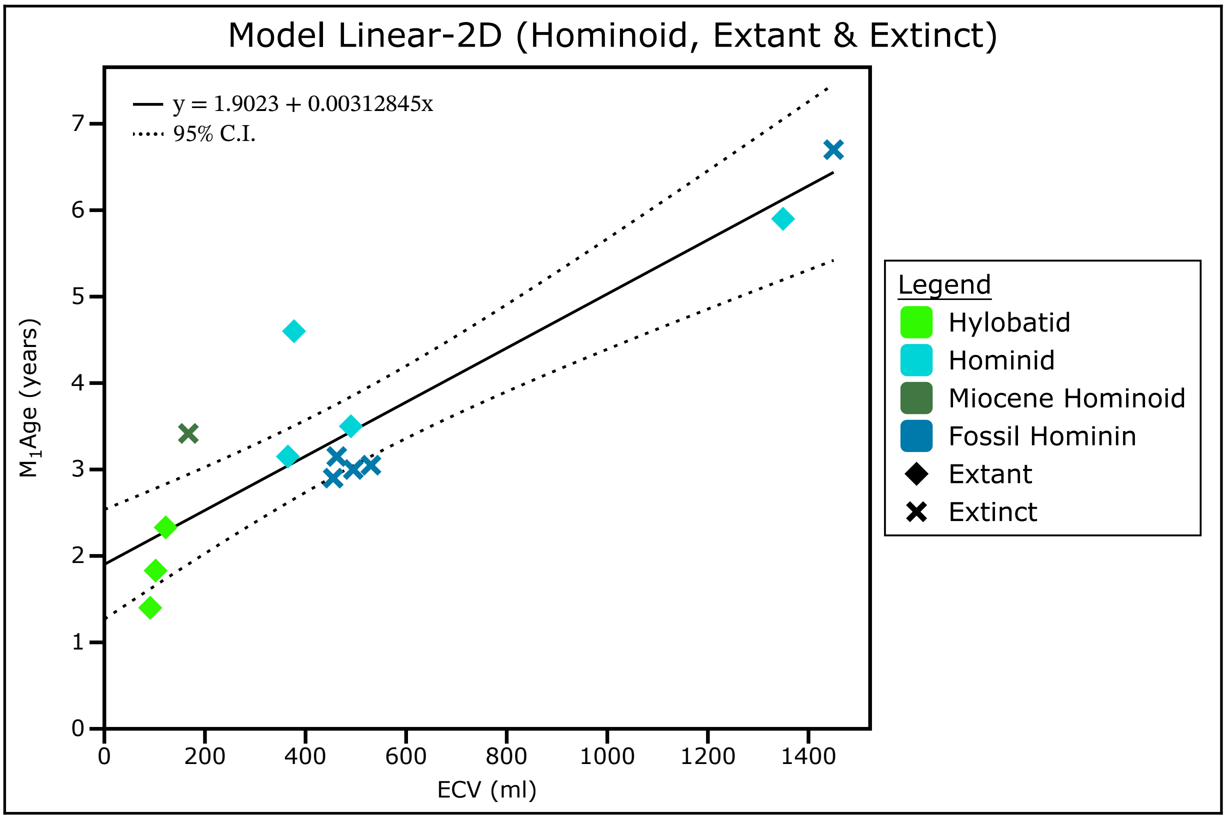

**Figure 5.21 Regression Plot: Linear-2D (Hominoid, Extant & Extinct)**

Model Linear-2D (Hominoid, Extant & Extinct): scatterplot for the extant & extinct hominoid sample (derived from 13 hominoid species, $r = 0.90$, $r^2 = 0.81$, $p < 0.001$, $s_e = 0.666$).

Main line represents the least squares regression line, where y is $M_1$Age (years) and x is endocranial volume (ml).

Dotted lines represent the upper and lower 95% confidence intervals.

Model Linear-2D predicts $M_1$Age as follows: *H. erectus* = 4.8 yr; *H. sapiens* = 6.1 yr; *P. troglodytes* = 3 yr.

Within the Linear Set 2 models, the coefficient of determination is greater in Model Linear-2C (Catarrhine). Within the Group-2D models, the coefficient of determination in the third level polynomials is greater than in all other models.

### Section 5.2.4.C Model Linear-2D (Hominoid, Extant & Extinct)

Model Linear-2D (Hominoid, Extant & Extinct) was created using a linear regression with the extant & extinct hominoid species data points (without ln-transformation). Model Linear-2D produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 1.902296 + 0.003128\, x$$

Model Linear-2D has a very highly positive correlation ($r = 0.90$, $p < 0.001$, $s_e = 0.666$). Model Linear-2D pred-$M_1$Age is within RC for *H. erectus*

(4.8 yr), and is within AC for *H. sapiens* (6.1 yr) and *P. troglodytes* (3 yr). Pred-$M_1$Age is within RC for *H. neanderthalensis* (6.4 yr) and Australopiths (3.4 yr), and is over-predicted above Fossil *H. sapiens* (6.6 yr).

The Model Linear-2D *H*-residual = -0.225 and *P*-residual = 0.106. *H*a-$M_1$Age is within AC for *H. erectus* (4.6 yr). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.3 yr) and *H. neanderthalensis* (6.2 yr), and is within AC for Australopiths (3.2 yr). *P*a-$M_1$Age is within RC but outside AC for *H. erectus* (4.9 yr). *P*a-$M_1$Age is within AC for *H. neanderthalensis* (6.5 yr), is within RC for the Australopiths (3.5), and is over-predicted above RC for Fossil *H. sapiens* (6.7). Model Linear-2D (Hominoid, Extant & Extinct) meets the stage 1 criteria. A comparision table of the Group 2D pred-$M_1$Ages is included below.

|  | **ln-2D** | ***H*-ADJUSTED ln-2D** | **QUAD-2D** | ***H*-ADJUSTED QUAD-2D** | **LINEAR-2D** | ***H*-ADJUSTED LINEAR-2D** |
|---|---|---|---|---|---|---|
| *P. troglodytes* | 3.2 | — | 3.0 | — | 3.0 | — |
| *H. sapiens* | 5.6 | — | 5.9 | — | 6.1 | — |
| *H. erectus* | 4.8 | 5.1 | 4.8 | 4.7 | 4.8 | 4.6 |
| Australopiths | 3.6 | 3.8 | 3.4 | 3.6 | 3.4 | 3.2 |
| *H. neanderthalensis* | 5.7 | 6.1 | 6.1 | 5.6 | 6.4 | 6.2 |
| Fossil *H. sapiens* | 5.8 | 6.1 | 6.2 | 5.7 | 6.6 | 6.3 |

**TABLE 5.7 GROUP 2D (HOMINOID, EXTANT & EXTINCT): PREDICTED $M_1$AGE**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H*a-$M_1$Ages for each.

## Section 5.2.5 Models, Group 2E (Hominid, Extant & Extinct)

Like the Group 1E Models (Hominids, Extant), the sample size is very small when only using the Hominid species. In Group 2E (Hominids, Extant & Extinct), adding fossil hominin data points increased the sample size very slightly. The model Quad-2E (Hominids, Extant and Extinct) met the inclusion criteria (described in Section 4.2) and the Model Linear-2E was borderline for the criteria ($p = 0.001$), which allowed for comparison of two models from Group 2E (Hominids, Extant & Extinct).

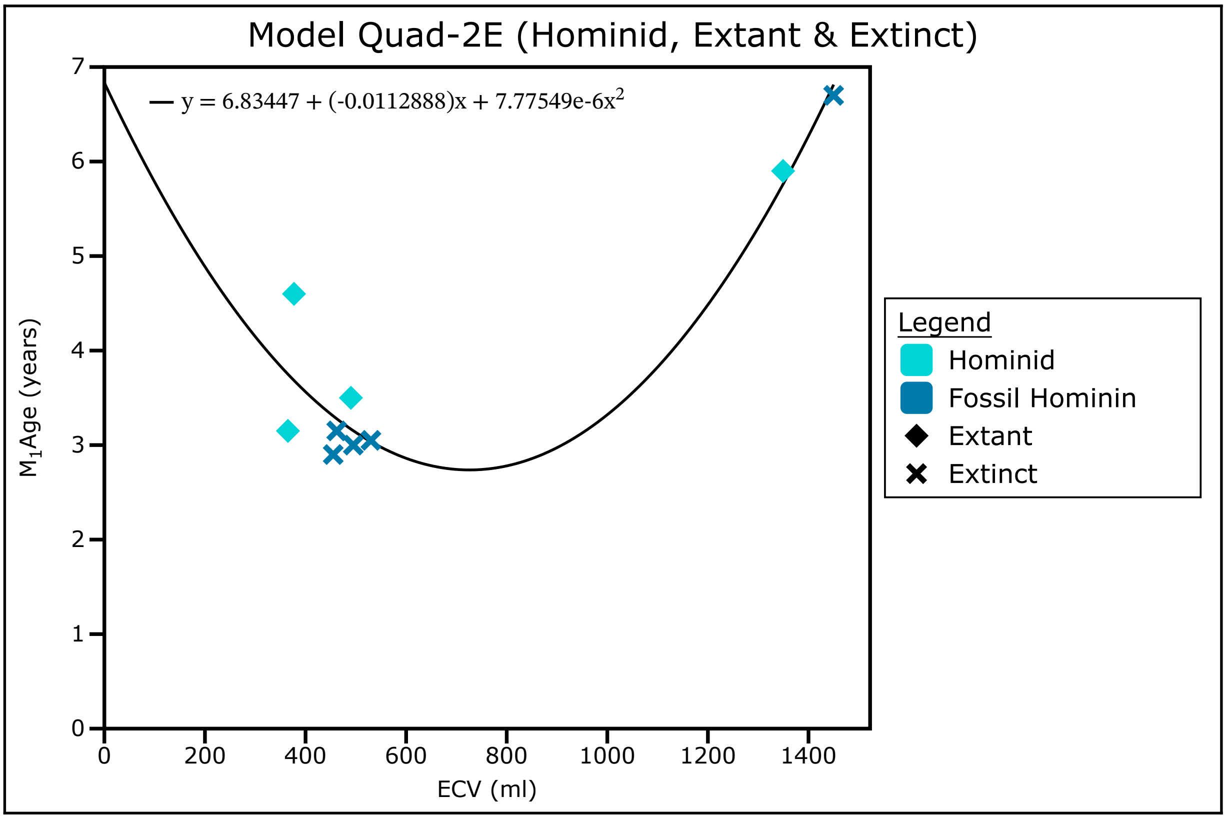

**Figure 5.22 Regression Plot: Quad-2E (Hominid, Extant & Extinct)**
Model Quad-2E (Hominid, Extant & Extinct): scatterplot for the extant & extinct hominid sample (derived from 9 hominid species, $r^2 = 0.90$, $p < 0.001$, $s_e = 0.803$). Solid line represents the second level polynomial equation regression line, where y is $M_1$Age (years) and x is endocranial volume (ml).
Model Quad-2E pred-$M_1$Ages are as as follows: *H. erectus*= 3.1; *H. sapiens* = 5.8, and *P. troglodytes* = 3.8. Within the Quad Set 2 (Extant & Extinct) models, the coefficient of determination is greater in Model Quad-2B (Haplorhine). Within the Group-2E models, the coefficient of determination in the second level polynomial model is greater than the first level (linear) model (the other two models, inclusive of Model Cubic-2E, have a p-value>0.001).

## Section 5.2.5.A Model Quad-2E (Hominid, Extant & Extinct)

Model Quad-2E (Hominid, Extant & Extinct) was created using a second degree polynomial regression with the extant & extinct hominid species data points. Model Quad-2E produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 6.834467 - 0.011289\,x + 0.000007775\,x^2$$

Model Quad-2E has a very highly positive correlation (R=0.95, p<0.001, $s_e$**=**0.803). Model Quad-2E pred-$M_1$Age is within AC for *H. sapiens* (= 5.8 yr) and outside RC for *H. erectus* (3.1) and *P. troglodytes* (3.8). Pred-$M_1$Age is predicted within AC for *H. neanderthalensis* (6.8) and the Australopiths (3.2), and is over-predicted above RC for Fossil *H. sapiens* (7.2).

The Model Quad-2E *H*-residual = 0.136 and *P. troglodytes* = –0.599. *H*a-$M_1$Age is under-predicted below RC for *H. erectus* (3.2). *H*a-$M_1$Age is within RC for the Australopiths (3.3) and *H. neanderthalensis* (7), and is over-predicted above RC for Fossil *H. sapiens* (7.4). *P*a-$M_1$Age is under-predicted below RC for *H. erectus* (2.5). *P*a-$M_1$Age is within RC for *H. neanderthalensis* (6.2); the Australopiths (2.6), and is over-predicted above RC for Fossil *H. sapiens* (6.6). Model Quad-2E (Hominid, Extant & Extinct) does not meet the stage one criteria.

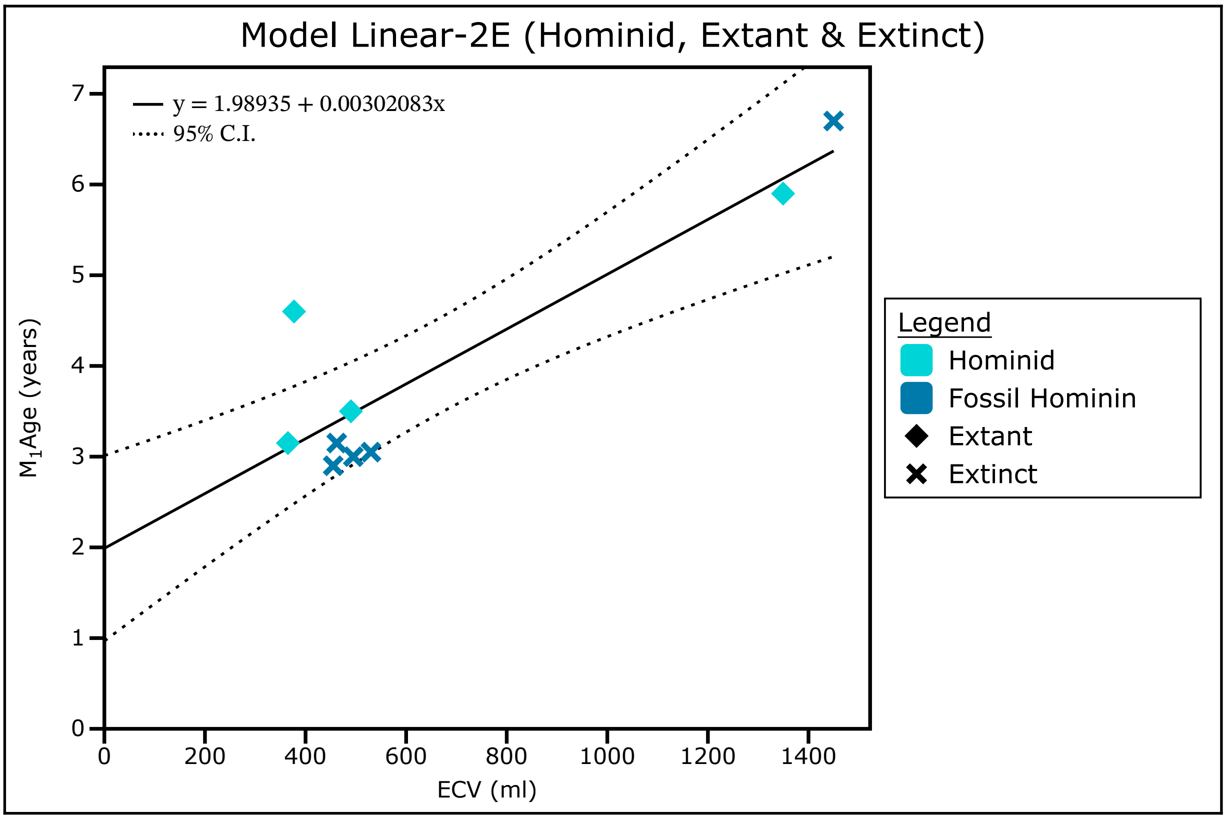

**FIGURE 5.23 REGRESSION PLOT: LINEAR-2E PLOT (HOMINID, EXTANT & EXTINCT)** Model Linear-2E (Hominid, Extant & Extinct): scatterplot for the extant & extinct hominid sample (derived from 9 hominid species, $r = 0.90$, $r^2 = 0.81$, $p = 0.001$, $s_e = 0.666$). Solid line represents the least squares regression line, where y is $M_1$Age (years) and x is endocranial volume (ml). Dotted lines represent the upper and lower 95% confidence intervals. Model Linear-2E predicts M1Age as follows: *H. erectus* = 4.8 yr; *H. sapiens* = 6.1 yr; *P. troglodytes* = 3.1 yr. Within the Linear Set 2 models, the coefficient of determination is greater in Model Linear-2C (Catarrhine). Within the Group-2E models, the coefficient of determination in the second level polynomial model is greater than the first level (linear) model (the other two models have p-value > 0.001).

## Section 5.2.5.B Model Linear-2E (Hominid, Extant & Extinct)

Model Linear-2E (Hominid, Extant & Extinct) was created using a linear regression with the extant & extinct hominid species data points (without ln-transformation). Model Linear-2E produced the following equation (where y is $M_1$Age in years and x is ECV in ml):

$$y = 1.989346 + 0.003021x$$

Linear-2E has a highly positive correlation ($r = 0.90$, $p = 0.001$, $s_e$=0.666). Linear-2E pred-$M_1$Age is within RC for *H. erectus* (4.8) and *H. sapiens* (6.1), and is within AC for *P. troglodytes* (3.1). Pred-$M_1$Age is within RC for *H. neanderthalensis* (6.4) and Australopiths (3.5), and over-predicted above RC for Fossil *H. sapiens* (6.5). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.3), *H. neanderthalensis* (6.2), and the Australopiths (3.3).

The Model Linear-2E *H*-residual = -0.167 and *P*-residual = 0.058. *H*a-$M_1$Age is within RC for *H. erectus* (4.7). *H*a-$M_1$Age is within RC for Fossil *H. sapiens* (6.3), *H. neanderthalensis* (6.2), and the Australopitsh (3.3). *P*a-$M_1$Age is within RC for *H. erectus* (4.9). *P*a-$M_1$Age is within RC for *H. neanderthalensis* (6.4) and the Australopiths (3.5), but is over-predicted above RC for Fossil *H. sapiens* = (6.5). Model Linear-2E (Hominid, Extant & Extinct) meets the stage one criteria. A comparison table of pred-$M_1$Ages from Group 2E is included below.

| | **Quad-2E** | **Linear-2E** | ***H*a-$M_1$Age Quad-2E** | ***H*a-$M_1$Age Linear-2E** |
|---:|:---:|:---:|:---:|:---:|
| *P. troglodytes* | 3.8 | 3.1 | — | — |
| *H. sapiens* | 5.8 | 6.1 | — | — |
| *H. erectus* | 3.1 | 4.8 | 3.2 | 4.7 |
| Australopiths | 3.2 | 3.5 | 3.3 | 3.3 |
| *H. neanderthalensis* | 6.8 | 6.4 | 7 | 6.2 |
| fossil *H. sapiens* | 7.2 | 6.5 | 7.4 | 6.3 |

**Table 5.8 Group 2E (Hominid, Extant & Extinct): Predicted $M_1$Age**
Comparison table of predicted $M_1$Age (years) for selected hominins (listed in Chapter 4) generated from the models presented in the above section, including the *H*a-$M_1$Ages for Linear-2D.

## Section 5.3 Accuracy of Models

To review the previous two sections of this chapter (5.1 and 5.2): when using the extant primate data points, the following models meet RC criteria for *H. erectus* $M_1$Age (4.4 ± 0.5 yr), without adjustment are:

- Model Cubic-1B (Haplorhine, Extant Only)
- Model Cubic-1C (Catarrhine, Extant Only)

The extant primate data models which improve accuracy or meet RC for *H. erectus* after adjustment are:

- Model ln-1A (Primate, Extant Only), meets after
- Model Linear-1C (Catarrhine, Extant Only), improves

When using fossil and subfossil primate data points to build a model, the following models meet RC for *H. erectus* $M_1$Age, without adjustment:

- Model ln-2D (Hominoid, Extant & Extinct)
- Model Quad-2D (Hominoid, Extant & Extinct)
- Model Linear-2C (Catarrhine, Extant & Extinct)
- Model Linear-2D (Hominoid, Extant & Extinct)
- Model Linear-2E (Hominid, Extant & Extinct)

When adding in the fossil and subfossil primate data points these models improve or meet RC for *H. erectus* $M_1$Age, after adjustment:

- Model ln-2A (Primate, Extant & Extinct)
- Model Quad-2D (Hominoid, Extant & Extinct)
- Model Linear 2B (Haplorhine, Extant & Extinct)
- Model Linear-2C (Catarrhine, Extant & Extinct)

- Model Linear-2D (Hominoid, Extant & Extinct)

Before moving on to presenting the $M_1$Age predictions for the fossil hominin ECV array, it may be helpful to review a summary of the performance of all 40 models. Using the first step of the stage one criteria (see Section 4.2.2), only 30 of the 40 models pass. Of those 30 models, only 28 are within range for at least one of either *P. troglodytes* or *H. sapiens* (19 of those 28 are in range for both *P. troglodytes* and *H. sapiens*). Of those 28 models, 9 models predict $M_1$Age within stage one criteria range for *H. erectus;* another 10 models are within stage one criteria range for *H. erectus* only with adjustment with the *H. sapiens*-residual. So that's a combined 19 models which predict $M_1$Age for *H. erectus* and at least one of either *P. troglodytes* or *H. sapiens* within stage one range.

The next stage addresses accuracy. Of those 19 models, 8 models predict *H. erectus* $M_1$Age within AC range (2 without adjustment, and 6 after adjustment). The two models which are *H. erectus*-accurate without adjustment are accurate for *H. sapiens* but not for *P. troglodytes*. In the other 6 of these 8 *H. erectus*-accurate models, 3 are accurate for *P. troglodytes* and 2 are accurate for *H. sapiens,* but none are accurate for both. Do models which are accurate for *H. erectus* also predict accurately for other three fossil hominins: Australopiths, *H. neanderthalensis*, and fossil *H. sapiens*. Of the 8 *H. erectus*-accurate models, all predict at least one of the other three fossil hominins within stage one range, and 4 of those are within stage one range for all three other fossil hominins. Of the 8 *H. erectus*-accurate models only 2 predict accurately for at least one of the other fossil hominins, and none predict accurately for more than one. While some of the models are deemed by the criteria to be accurate for *H. erectus,* none of the "*H. erectus*-accurate" models are simultaneously accurate across fossil hominins, even when those species are used in the model, and even with ad-hoc adjustments.

Potentially this would be because *H. erectus* varies from the line of regression differently than the other hominins. Are any of the models accurate for the other fossil hominins without being accurate for *H. erectus*? Of the 30 models which pass the first half of the stage one criteria ($r \geq 0.80$, $p \geq 0.001$), 8 models are accurate for at least one fossil hominin without being accurate for *H. erectus*. Where models are not "*H. erectus*-accurate" after adjustments are applied: 8 models are accurate for at least one fossil hominin after adjustment with the *H. sapiens*-residual; 7 models are accurate for at least one fossil hominin after adjustment with the *P. troglodytes*-residual. There is some overlap, so across the three categories just mentioned, there are a combined 21 models. Of these 21 models, only 2 are accurate for more than one fossil hominin: one after adjustment with *H. sapiens*-residual (Australopiths and fossil *H. sapiens*); one after adjustment with *P. troglodytes*-residual (Australopiths and *H. neanderthalensis*). Either with or without accuracy for *H. erectus*, there is no model which is accurate for both *H. neanderthalensis* and fossil *H. sapiens* at the same time. Where *H. neanderthalensis* is accurate, fossil *H. sapiens* is over-predicted. Where fossil *H. sapiens* is accurate, *H. neanderthalensis* is under-predicted. This includes models accurate for either after adjustment with the *H*-residual or or *P*-residual.

# Chapter 6

# Chapter 6 $M_1$ Age Prediction Results

In the preceding sections, the regression plots for selected models were presented. This section now presents a more detailed look at the predictions created by these models when applied a larger set of fossil hominin ECVs. As before, the models will be presented in sections by Group (1B, 1C, 2D and 2E), followed by a brief review of issues or variations in the predictions. In the following figures, the various *Homo* species/subspecies represented are grouped together primarily by geological age. *H. e. erectus* specimens are further divided into regional groups (see Figure 4.14).

Individual specimens within the *H. habilis/rudolphensis* group fall metrically outside the group, pulling up the group's range and mean (see Appendix Table 9.5.). *H. e. ergaster* falls temporally within the Early *Homo* Group*.* However, the 3 *H. e. ergaster* ECVs fall metrically within the African *H. e. erectus* group. *H. e. ergaster's* placement within the Early *Homo* Group is not a phylogenetic placement: the intention is to contrast how fossils with overlapping ECVs are predicted differently by regressions to emphasise the issues which arise when making implications based on the apparent differences between each prediction. This study considers *H. e. ergaster* and *H. e. georgicus* to be paleo-demes of *H. erectus* s.l.: a polymorphic species which had an extensive geographic and temporal range. As such, they are separated within the box plots to highlight any issues or patterns with how these populations are predicted for when treated as a separate species. Where possible, I have tried to layout the box-plot graphs with the individual sub-section describing the relevant results. The box plots generally precede the text for each sub-section (e.g. the ln-1A box plot is followed by the section for ln-1A).

As noted previously, predictions have been generated for all 40 models, using the ECV mean for each of three species (*P. troglodytes, H. s. sapiens,* and *H. e. erectus*), but only the regression plots and details for the models which met inclusion criteria are now discussed in this next stage. In the next stage, box plots of the predictions generated when the included models are applied to the larger fossil hominin ECV data set (see Appendix). The models being discussed next (which have either met the inclusion criteria[34] or are used as comparison with those models are):

- ln-Models (adjusted): ln-1A; ln-1B; ln-1C; ln-2A; ln-2B; ln-2C; ln-2D
- Cubic Models: Cubic-1A, Cubic-1B, Cubic-1C
- Quadratic-Models: Quad-2C (adjusted); Quad-2D; Quad-2E
- Linear-Models (adjusted): Linear-1A; Linear-1B; Linear-1C, Linear-2D, Linear-2E.

In the following box & whisker plots, species boxes are grouped by species (or sub-species/paleo-deme) which are display in 5 groups (as outlined in Section 4.2). Within each group, the species bars are coloured in a darker shade of the group colour and the lighter coloured box behind each group denotes the range of that grou*p.* Within each species box, the box indicates the interquartile range, the “whiskers” above and below mark the minimum and maximum, the

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[34] see Section 4.2

species median is marked with a line and the species mean is marked with an X. In some instances, the range is so small that the line and x have been suppressed.

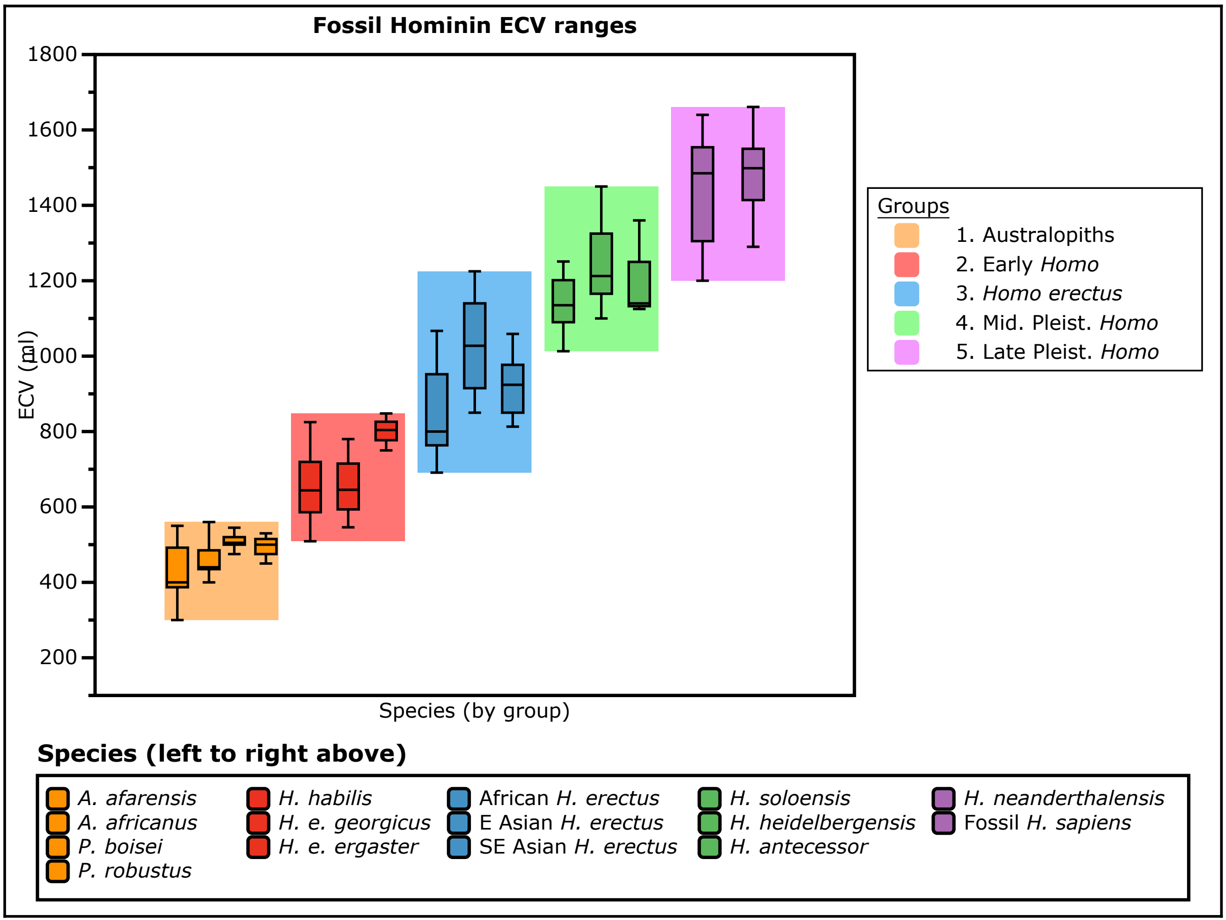

**Figure 6.1 Fossil Hominin ECV Ranges**

Box and whisker plots of ECV (ml) of individual fossil hominin specimens.

Because pred-$M_1$Age ranges are derived from ECV values, these box plots are provided as a comparison to refer to when looking at how narrowly or widely pred-$M_1$Age plots in the models which are presented in Section 6.1 and Section 6.2.

For instance: while the *H. e. erectus* group has the widest ECV range, pred-$M_1$Age range for this group does not always plot more widely than pred-$M_1$Age ranges of other fossil hominin groups.

Please note, this is not a plot of findings from this study, it is a plot of the distribution of ECV values used by this study to generate pred-$M_1$Ages. This is provided as a visual reference.

## Section 6.1 Set 1 Models (Extant Only)

### Section 6.1.1 Group 1A (Primate, Extant Only)

In Chapter 5, the results show that the three Group 1A (Primate, Extant Only) models ( ln-1A, Cubic-1A, and Linear-1A) do not predict $M_1$Age within AC for all 4 main fossil hominin $M_1$Age cases (*H. erectus,* Australopiths, *H. neanderthalensis*, Fossil *H. sapiens*). In this section, pred-$M_1$Ages for the range of fossil hominin ECV are presented individually. A short summary of comparisons between the models will follow at the end of the third model's subsection.

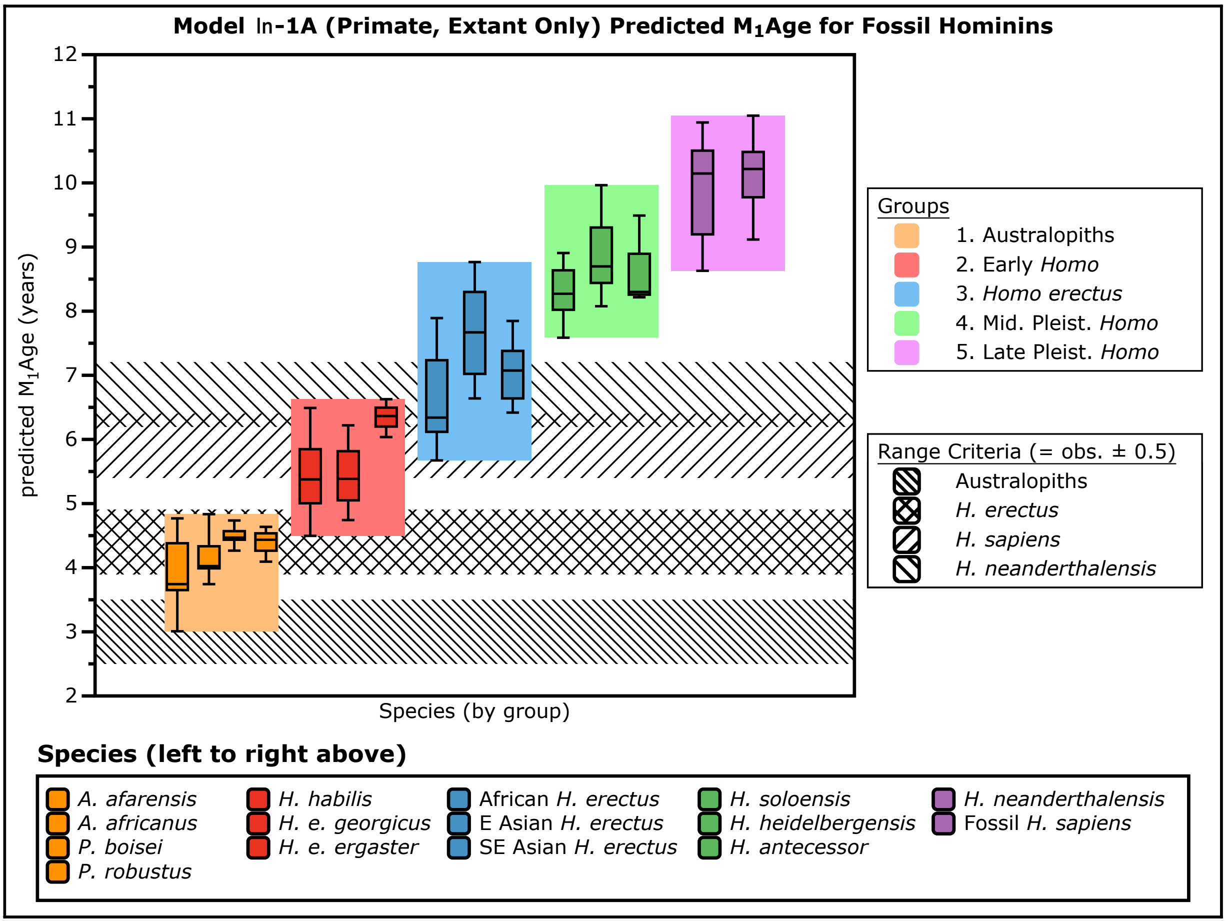

**Figure 6.2 Box & Whisker Plot: ln-1A (Primate, Extant Only)**
Model ln-1A (Primate, Extant Only) does not meet the primary range criteria.
Model ln-1A *H. e. erectus* group pred-$M_1$Age (years) = 7.2 yr (median = 7.2, 5.7—8.8; African *H. erectus* = 6.7; East Asian *H. erectus* = 7.7; Southeast Asian *H. erectus* = 7.1). Pred-$M_1$Age for the remaining groups is as follows: Australopiths = 4.2 (median = 4.3, 3.0—4.8); Early *Homo* = 5.6 (median = 5.4, 4.5—6.6); Middle Pleistocene *Homo* = 5.4 (median = 8.6, 7.6—10); Late Pleistocene *Homo* = 10 (median = 10.2, 8.6—11).

### Section 6.1.1.A Model ln-1A (Primate, Extant Only)

As noted in Chapter 5, Model ln-1A (Primate, Extant Only) does not meet the stage one inclusion criteria and does not predict $M_1$Age within RC for any of the fossil hominins. When applied to the full fossil ECV sample, the full extent of the over-prediction for fossil hominins can be seen (see Figure 6.2). The average pred-$M_1$Age for *H. e. erectus* as a group = 7.2 yr. The subgroup average pred-$M_1$Age is over-predicted well-above RC: African *H. erectus* = 6.7, East Asian *H. erectus* = 7.7, Southeast Asian *H. erectus* = 7.1. The average Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 4.2 yr; Early *Homo* = 5.6 yr; Middle Pleistocene = 8.7 yr; Late Pleistocene = 10.0 yr.

Because of the overlap in ECV between the African *H. erectus* and the *H. e. ergaster* fossils, *H. e. ergaster* predicted values fall inside of the African *H. erectus* predicted values. The *H. soloensis* fossils, which are grouped with SE Asian *H. e. erectus* fossils by some taxonomies, only have minor overlap with each other, and if they had been grouped together would have increased the predicted $M_1$Age upper spread for SE Asian *H. e. erectus* to above East Asian *H. e. erectus*. In Figure 6.2, it can be clearly seen that the three *H. e. erectus* sub-groups are all well above *H. erectus* RC, and all or most of the predicted $M_1$Age values in the Asian *H. e. erectus* sub-groups are above the *H. sapiens* RC. The Middle and Late Pleistocene *Homo* groups are considerably over-predicted by many years. Because of overlapping ECVs in *H. neanderthalensis* and Fossil *H. sapiens*, any given regression can potentially only ever predict one or the other within AC. However, in this case, both are well over RC by years.

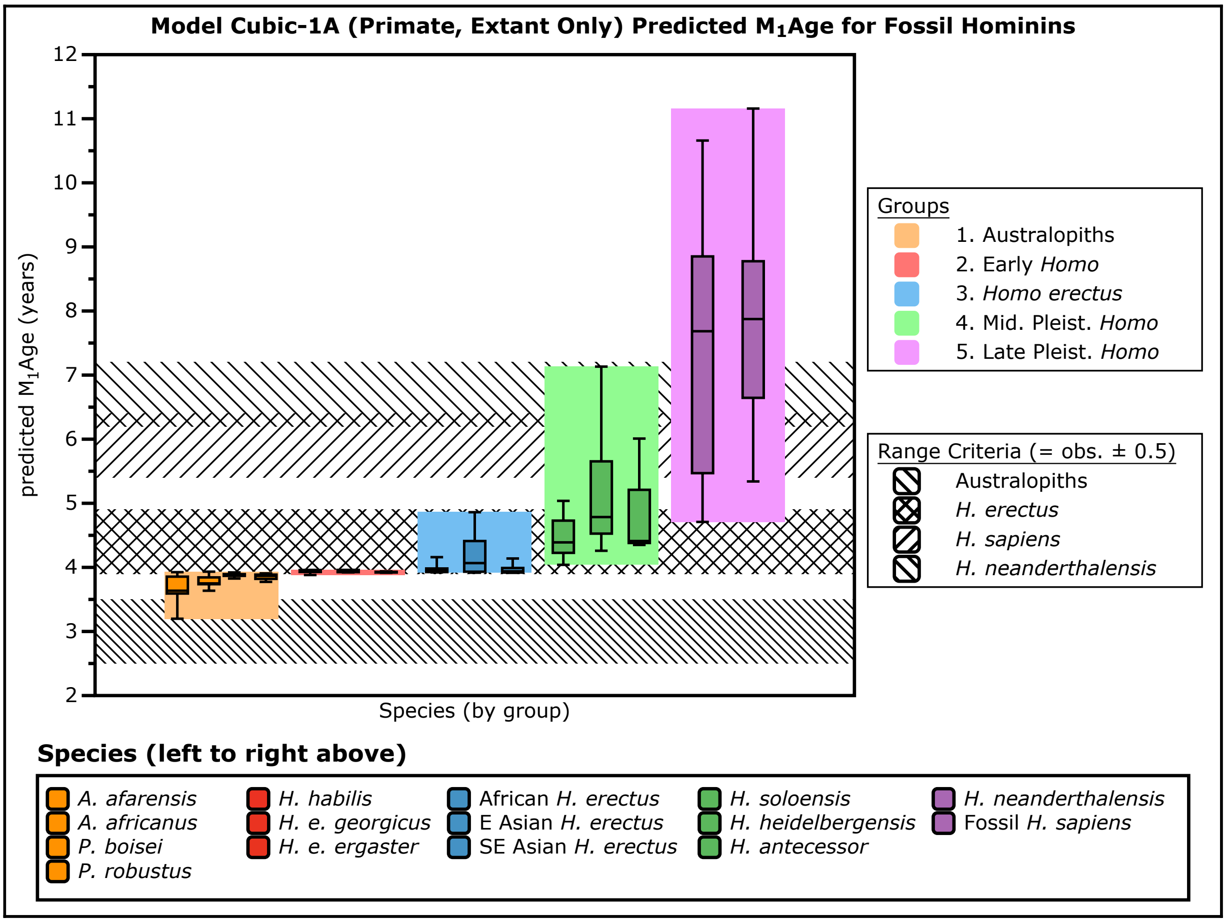

**Figure 6.3 Box & Whisker Plot: Cubic-1A (Primate, Extant Only)**

Model Cubic-1A (Primate, Extant Only) meets the primary range criteria. The Model Cubic-1A predicted $M_1$Age (years) for *Homo erectus* = 4.1 (median = 4.0 yr, range = 3.9—4.9), and for the *H. erectus* subgroups as follows: African *H. erectus* = 4.0; East Asian *H. erectus* = 4.2; Southeast Asian H. erectus = 4.0. The Model Cubic-1A predicted $M_1$Age (years) for the remaining fossil hominin groups is as follows: Australopiths = 3.8 (median = 3.8, range = 3.2—3.9); Early *Homo* = 3.9 (median = 3.9, range = 3.9—4.0); Middle Pleistocene *Homo* = 4.9 (median = 4.6, range = 4.0—7.1); Late Pleistocene *Homo* = 7.7 (median = 7.9, range = 4.7—11.2).

### Section 6.1.1.B Model Cubic-1A (Primate, Extant Only)

In Chapter 5, the results show Model Cubic-1A meets the stage one inclusion criteria. Pred-$M_1$Age is within RC for *H. erectus*, *H. sapiens*, and *P. troglodytes*. Pred-$M_1$Age is over-predicted in the other three fossil hominins.

When Cubic-1A is applied to the individual fossil specimen ECVs, the average Pred-$M_1$Age in the *H. e. erectus* group = 4.1 yr (African *H. erectus* = 4.0 yr, East Asian *H. erectus* = 4.2 yr, Southeast Asian *H. erectus* = 4.0 yr). Pred-$M_1$Age for the remaining groups are: the Australopiths = 3.8 yr; Early *Homo* = 3.9 yr; Middle Pleistocene = 4.9 yr; Late Pleistocene = 7.7 yr.

In Figure 6.3, the compressed spread of pred-$M_1$Ages in the lower three groups, compared to the very wide spread in Middle and Late Pleistocene groups. Cubic equation mid-range curves tend to look like a reversed sideways S curve (see Figure 5.2). In this model the middle of that curve is somewhat "flattened". This results in the vertical spread of pred-$M_1$Ages in the smaller three of the five groups being very compressed. All of the early *Homo* predictions appear to fall mostly within the African *H. erectus* prediction. On the higher end of the ECV range, $M_1$Age predictions appear to spike in relation to ECV increase, especially where an ECV value is greater than the modern *H. sapiens* ECV used to build the model (1350 ml). The Australopiths pred-$M_1$Ages are mostly over-predicted above Australopith RC, but still below the *H. erectus* RC. While Model Cubic-1A predicts *H. sapiens* $M_1$Age very nearly equal to observed, and both *H. erectus* and *P. troglodytes* within RC, the model does not predict accurately for fossil hominins as a whole.

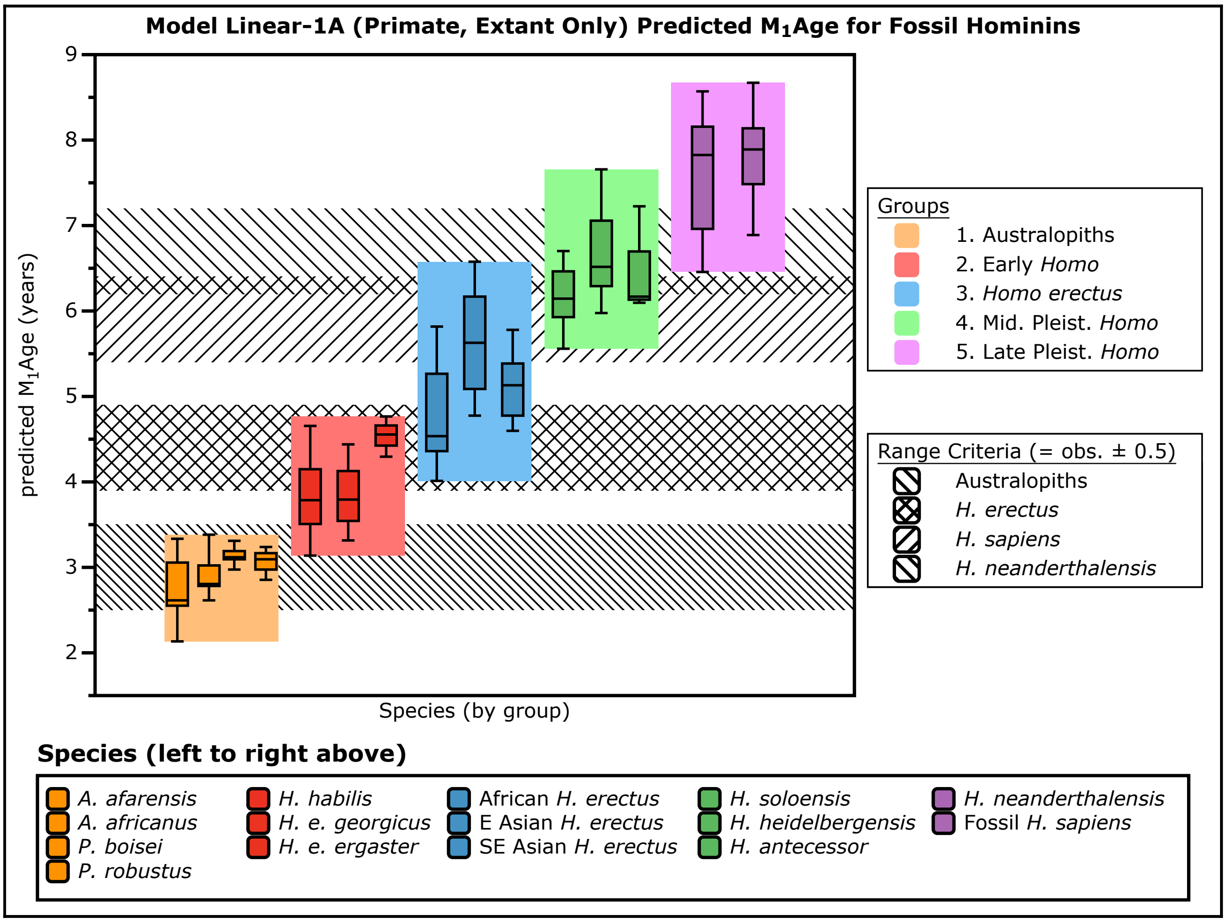

**FIGURE 6.4 BOX & WHISKER PLOT: LINEAR-1A (PRIMATE, EXTANT ONLY)**

Linear 1A (Primate, Extant Only) box plots, by species (grouped), of fossil hominin pred-$M_1$Age ranges.

Predicted $M_1$Age for the *H. e. erectus* group = 5.2 yr (median = 5.2, range= 4.0—6.6).

Pred-$M_1$Ages for the *H. e. erectus* regional subgroups as follows:

African *H. erectus* = 4.8*;*

East Asian *H. erectus* = 5.6;

Southeast Asian *H. erectus* = 5.2.

Model Linear-1A predicted $M_1$Age (yr) for the remaining groups are as follows:

Australopiths = 3 yr (median = 3, range = 2.1—3.4);

Early *Homo* = 4.0 yr (median = 3.8, range = 3.1—4.8);

Middle Pleistocene *Homo* = 6.5 yr (median = 6.4, range = 5.6—7.7);

Late Pleistocene *Homo* = 7.7 yr (median = 7.9, range 6.5—8.7)

### Section 6.1.1.C Linear-1A (Primate, Extant Only)

In Chapter 5, the results show that Model Linear-1A does not meet the stage one criteria. Model Linear-1A pred-$M_1$Age is only within RC for the Australopiths, and is over-predicted above RC for the other hominins. When applied to individual fossil specimen ECVs, pred-$M_1$Age of *H. e. erectus* group = 5.2 yr (African *H. erectus* = 4.8 yr, East Asian *H. erectus* = 5.6 yr, Southeast Asia *H. erectus* = 5.1 yr). Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.0 yr; Early *Homo* = 4.0 yr; Middle Pleistocene = 6.5 yr; Late Pleistocene = 7.7 yr.

In Figure 6.4, pred-$M_1$Ages for *H. e. erectus* are spread across both *H. erectus* RC and *H. sapiens* RC. All of the *H. e. ergaster* pred-$M_1$Ages are within *H. e. erectus* RC and would plot within the pred-$M_1$Age spread for African *H. e. erectus*. The Late Pleistocene group predicts above *H. sapiens* RC. The Australopiths are predicted mostly within RC, however Linear-1A doesn't predict $M_1$Age within AC for fossil *Homo* species as a whole.

## Summary

None of the above Models predict within accuracy range for all of the fossil hominin groups. Model Cubic-1A predicts all of the *H. e. erectus* sub-groups within RC, but the other groups are largely not within RC, and groups with fossils in the upper range for ECV are can be highly over-predicted. Model ln-1A over-predicts across all 5 groups. Model Linear-1A predicts mostly within RC for the Australopiths, but then the range for each following fossil hominin group reaches over-prediction or is over-predicted. Comparing Figure 6.2 (ln-1A) and Figure 6.4 (Linear-1A), it can be seen that using ln-transformed values for the Group 1A (Primate, Extant Only) data results in a larger amount of over-prediction above RC than performing a linear regression on the data without ln-transformation.

### Section 6.1.2 Group 1B (Haplorhine, Extant Only)

This section presents the three Group 1B (Haplorhine, Extant Only) Models: ln-1B, Cubic-1B, and Linear-1B. While Cubic-1B is within RC for the *H. e. erectus* group, and Linear-1B is largely within RC for the Australopiths group, no model is within RC for all groups. The three models are presented in sub-sections, followed by a short summary comparison of highlights from these models.

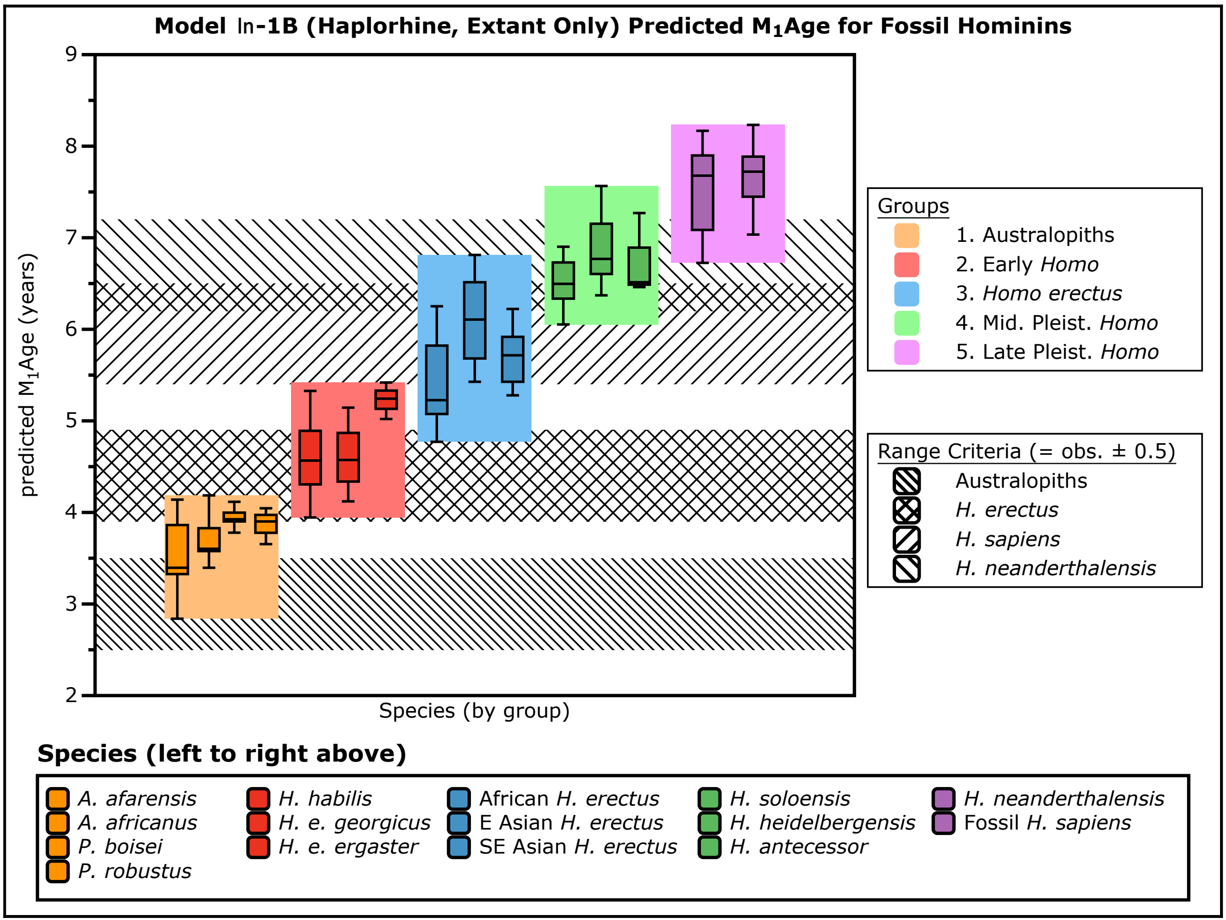

**FIGURE 6.5 BOX & WHISKER PLOT: ln-1B (HAPLORHINE, EXTANT ONLY)**
Model ln-1B (Haplorhine, Extant Only) box plots of fossil hominin pred-$M_1$Ages.
Pred-$M_1$Age for the *H. e. erectus* group = 5.8 yr (median = 5.8; range = 4.8—6.8)
Pred-$M_1$Ages for the regional *H. e. erectus* subgroups as follows:
African *H. erectus* = 5.4 yr*;*
East Asian *H. erectus* = 6.1 yr;
Southeast Asian *H. erectus* = 5.7 yr.
Model ln-1B pred-$M_1$Ages for the remaining groups are as follows:
Australopiths = 3.8 yr (median = 3.8, 2.8—4.2);
Early *Homo* = 4.7 yr (median = 4.6, 3.9—5.4);
Middle Pleistocene *Homo* = 6.8 yr (median = 6.7, 6.1—7.6);
Late Pleistocene *Homo* = 7.6 yr (median = 7.7, 6.7—8.2).

### Section 6.1.2.A Model ln-1B (Haplorhine, Extant Only)

In Chapter 5, the results showed that Model ln-1B (Haplorhine, Extant Only) does not meet the stage one criteria, and pred-$M_1$Age is over-predicted above RC for any of the 4 observed fossil hominins data points.

From the Model ln-1B box plots (Figure 6.5), the average pred-$M_1$Age is over-predicted above RC for the *H. e. erectus* group = 5.8 yr (African *H. erectus* = 5.4 yr, East Asian *H. erectus* = 6.1 yr, Southeast Asian *H. erectus* = 5.7 yr). The pred-$M_1$Age range for the *H. e. erectus* group begins at the top of RC for *H. erectus,* and the upper range for the group is well above the RC for *H. sapiens.* Group average pred-$M_1$Ages for the remaining fossil hominins are as follows: Australopiths = 3.8 yr; Early *Homo* = 4.7 yr; Middle Pleistocene = 6.8 yr; Late Pleistocene = 7.6 yr.

In Figure 6.5, *H. e. erectus* group's pred-$M_1$Age range plots from the top of the *H. erectus* RC, across the *H. sapiens* RC and half of the *H. neanderthalensis* RC. The Late Pleistocene group pred-$M_1$Ages are entirely above *H. sapiens* RC, and the upper range is as high as 8.2 years. With the exception of the lower range of *A. afarensis*, the Australopiths ranges are plotting mostly above Australopith RC, and into the lower half of *H. erectus* RC.

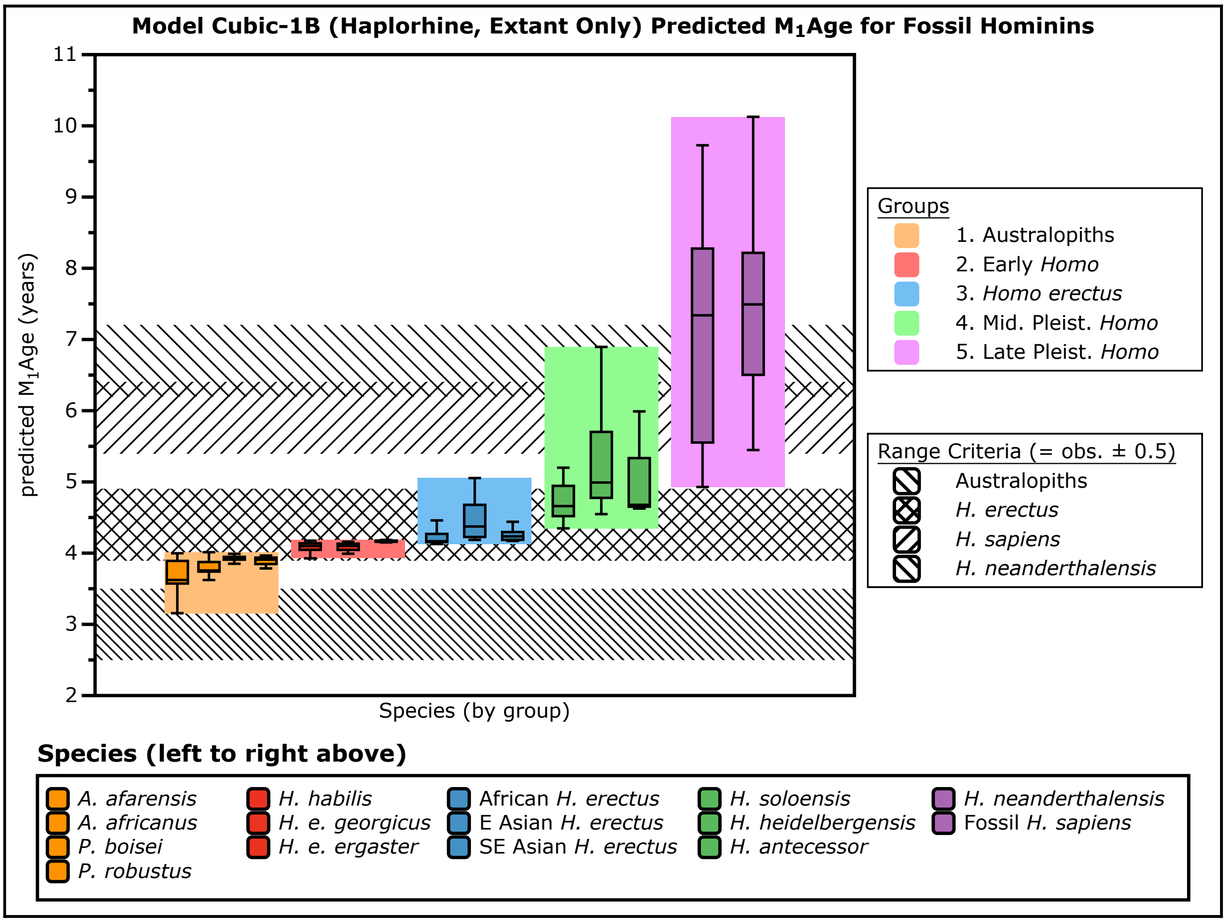

**FIGURE 6.6 BOX & WHISKER PLOT: CUBIC-1B (HAPLORHINE, EXTANT ONLY)**

Model Cubic-1B box plots of fossil hominin pred-$M_1$Ages.
Pred-$M_1$Age for the *H. e. erectus* group = 4.3 yr (median = 4.2, min = 4.1, max= 5.1).
Pred-$M_1$Ages for *H. e. erectus* regional subgroups as follows:
African *H. erectus* = 4.2 yr;
East Asian *H. erectus* = 4.5 yr;
Southeast Asian *H. erectus* = 4.3 yr.
Model Cubic-1B predicted $M_1$Age for the remaining groups is as follows:
Australopiths = 3.8 yr (median = 3.9, min = 3.2, max = 4.0);
Early *Homo* = 4.1 yr (median = 4.1, min = 3.9, max = 4.2);
Middle Pleistocene *Homo* = 5.1 yr (median = 4.9, min = 4.3, max = 6.9);
Late Pleistocene *Homo* = 7.3 yr (median = 7.5, min = 4.9, max = 10.1).

### Section 6.1.2.B Cubic-1B (Haplorhine, Extant Only)

In Chapter 5, the results show that Model Cubic-1B (Haplorhine, Extant Only) meets the stage one inclusion criteria, and pred-$M_1$Age is within AC for *P. troglodytes*, *H. sapiens*, *H. erectus*, and *H. neanderthalensis*, but pred-$M_1$Age is over-predicted above AC for the other fossil hominins. When predictions are made with individual fossil hominin ECVs, the *H. e. erectus* group the average pred-$M_1$Age = 4.3 yr (African *H. erectus* = 4.2 yr, East Asian *H. erectus* = 4.5 yr, Southeast Asian *H. erectus* = 4.3 yr). Most of the *H. e. erectus* group's pred-$M_1$Age range falls within RC. Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.8 yr; Early *Homo* = 4.1 yr; Middle Pleistocene = 5.1 yr. Late Pleistocene = 7.3 yr.

In Figure 6.6 the way that Cubic-1B increasingly over-predicts in the larger ECVs as ECV increases above extant *H. sapiens* ECV of 1350 ml used to build the model is evident. Pred-$M_1$Age for the Late Pleistocene group ranges as high as 10.1 yr). Pred-$M_1$Age in the Early *Homo* group is a compressed range which and falls within *H. erectus* RC. Most of pred-$M_1$Age for the Australopiths is above RC. While the *H. e. erectus* group is predicted largely within *H. erectus* RC, this model does not predict $M_1$Age within accuracy for the majority of the rest of the fossil hominin groups. Contrasted with the how the ranges of *H. e. erectus* ECV plot compared to the Late Pleistocene *Homo* group (presented in Figure 6.1), the pred-$M_1$Age range for *H. e. erectus* is plotted in a much narrower range than the pred-$M_1$Age range for the Late Pleistocene group.

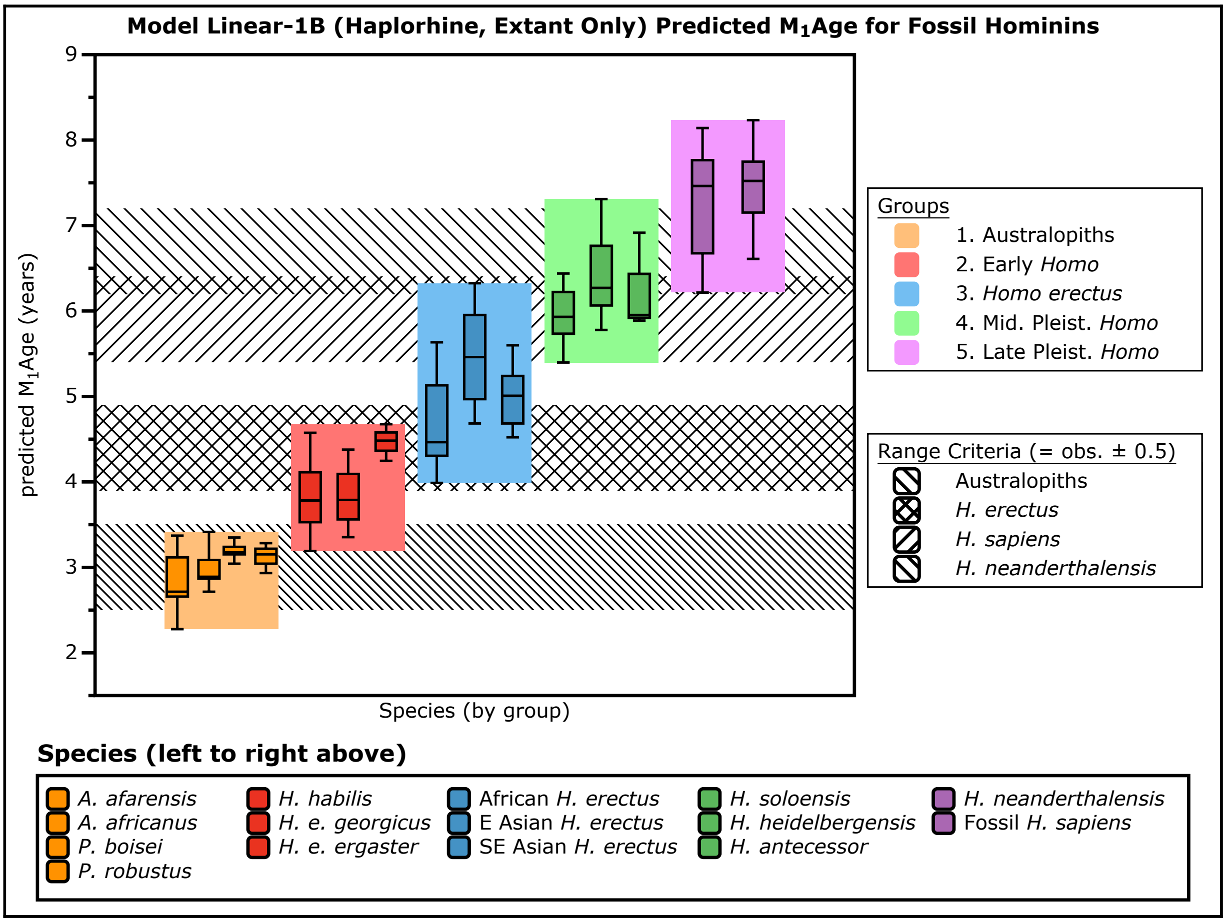

**FIGURE 6.7 BOX & WHISKER PLOT: LINEAR-1B (HAPLORHINE, EXTANT ONLY)**
Model Linear-1B box plots of fossil hominin pred-M$_1$Ages.
Pred-M$_1$Age the *H. e. erectus* group = 5.1 yr (median = 5.1; range 4.0—6.3)
Pred-M$_1$Ages for the *H. e. erectus* subgroups as follows:
African *H. erectus* = 4.7 yr;
East Asian *H. erectus* = 5.5 yr;
Southeast Asian *H. erectus* = 5.0 yr.
Pred-M$_1$Age for the remaining groups are as follows:
the Australopiths = 3.0 yr (median = 3.1, 2.3—3.4);
Early *Homo* = 4.0 yr (median = 3.8, 3.2—4.7);
Middle Pleistocene = 6.3 yr (median = 6.2, 5.4—7.3);
Late Pleistocene = 7.4 yr (median = 7.5, 6.2—8.2).

### Section 6.1.2.C Linear-1B (Haplorhine, Extant Only)

In Chapter 5, the results show that Model Linear-1B does not meet the stage one inclusion criteria. Model Linear-1B pred-$M_1$Age is within AC for the Australopiths, but is over-predicted above RC for the other fossil hominins.

The average pred-$M_1$Age in the *H. e. erectus* group = 5.1 yr (African *H. erectus* = 4.7 yr, East Asian *H. erectus* = 5.5 yr, Southeast Asian *H. erectus* = 5.0 yr). Pred-$M_1$Age for the remaining groups are as follows: the Australopiths = 3.0 yr; Early *Homo* = 4.0 yr; Middle Pleistocene = 6.3 yr; Late Pleistocene = 7.4 yr.

In Figure 6.7, it can be seen that, Pred-$M_1$Age for the Australopiths is largely within RC. *H. e. erectus* pred-$M_1$Age shows a wide range from within *H. erectus* RC to as high as the upper range of the RC for *H. sapiens*. Some of Middle Pleistocene group pred-$M_1$Age is within *H. sapiens* RC, however *H. heidelbergensis* and *H. antecessor* range above *H. sapiens* RC. Late Pleistocene group pred-$M_1$Age is almost entirely above *H. sapiens* RC, and as with all previous models, this model does not predict the observed $M_1$Age variation between these two *Homo* species which overlap in the majority of their ECV ranges.

## Summary

Cubic-1B appears within RC for most of the *H. e. erectus* range, but over-predictions increase in fossil hominins with ECV above the *H. e. erectus* group, and greatly increase in fossil hominins with ECV above 1350 ml. Comparing Figure 6.5 (Model $\ln$-1B) to Figure 6.7 (Model Linear-1B), ranges appear less over-predicted when using the data un-transformed, but there is still a large amount of over-prediction. No Group 1B (Haplorhine, Extant Only) model has pred-$M_1$Age ranges which are accurate for all of the fossil hominin groups.

### Section 6.1.3 Prediction results for Group 1C (Catarrhine, Extant)

This section presents the three Group 1C (Catarrhine, Extant Only) Models: ln-1C, Cubic-1C, and Linear-1C. The three models are presented in sub-sections, followed by a short summary comparison of highlights from these models.

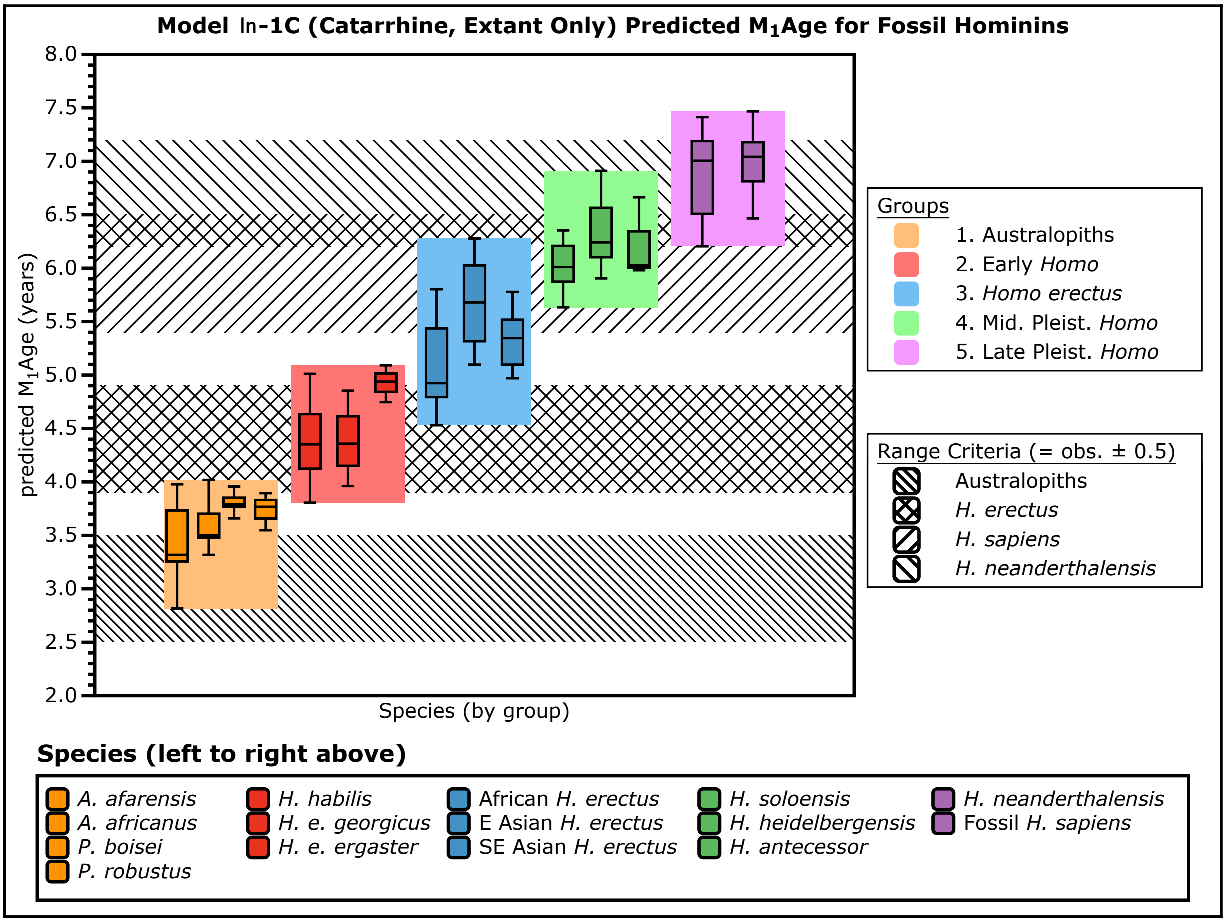

**Figure 6.8 Box & Whisker Plot: ln-1C (Catarrhine, Extant Only)**
Model ln-1C (Catarrhine, Extant Only) box plots of fossil hominin pred-$M_1$Ages.
Pred-$M_1$Age the *H. e. erectus* group = 5.4 yr (median = 5.4; range 4.5—6.3).
Pred-$M_1$Age for the *H. e. erectus* sub-groups are as follows:
African *H. erectus* = 5.1 yr
East Asian *H. erectus* = 5.7 yr
Southeast Asian *H. erectus* = 5.3 yr.
Pred-$M_1$Age for the remaining groups are as follows:
the Australopiths = 3.6 yr (median = 3.7, 2.8—4.0);
Early *Homo* = 4.5 yr (median = 4.4, 3.8—5.1);
Middle Pleistocene = 6.2 yr (median = 6.2, 5.6—6.9);
Late Pleistocene = 7.0 yr (median = 7.0, 6.2—7.5).

### Section 6.1.3.A Model ln-1C (Catarrhine, Extant)

In Chapter 5, the results show that Model ln-1C (Catarrhine, Extant Only) does not meet the stage one criteria, and show that pred-$M_1$Age is within RC only with *H. neanderthalensis* and is not within AC for any fossil hominin. Looking now at the average pred-$M_1$Age for the fossil hominin groups, the *H. e. erectus* group = 5.4 yr (median = 5.4; min = 4.5; max = 6.3) and the *H. e. erectus* sub-groups are as follows: African *H. erectus* = 5.1 yr, East Asian *H. erectus* = 5.7 yr, Southeast Asian *H. erectus* = 5.3 yr. Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.6 yr (median = 3.7, min = 2.8, max = 4.0); Early *Homo* = 4.5 yr (median = 4.4, min = 3.8, max = 5.1); Middle Pleistocene = 6.2 yr (median = 6.2, min = 5.6, max = 6.9). Late Pleistocene = 6.9 yr (median = 7.0, min = 6.2, max = 7.5).

In Figure 6.8, *H. e. erectus* group plots from within the top end of the *H. erectus* RC and through most of *H. sapiens* RC. The Late Pleistocene group plots within *H. neanderthalensis* RC and mostly above *H. sapiens* RC. Three of the four of Australopith species pred-$M_1$Age ranges plot mostly or entirely above Australopith RC.

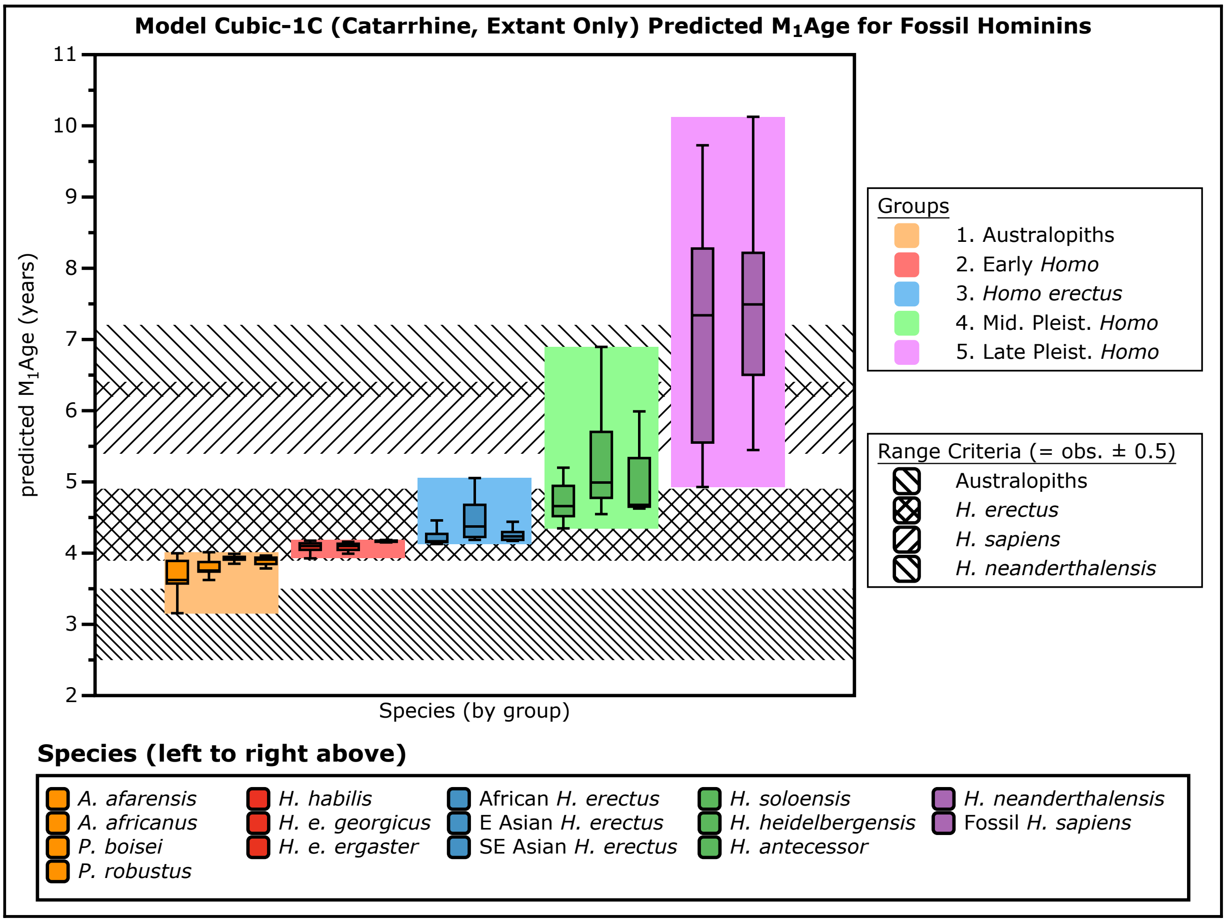

**FIGURE 6.9 BOX & WHISKER PLOT: CUBIC-1C (CATARRHINE, EXTANT ONLY)**

Model Cubic-1C box plots, by species (grouped), of fossil hominin pred-M$_1$Ages.
Pred-M$_1$Age for the *H. e. erectus* group = 4.3 yr (median = 4.2 yr, min = 4.1, max= 5.1).
Pred-M$_1$Ages for the *H. e. erectus* regional subgroups are as follows:
African *H. erectus* = 4.2 yr;
East Asian *H. erectus* = 4.5 yr;
Southeast Asian *H. erectus* = 4.3 yr.
Pred-M$_1$Ages for the remaining fossil hominin groups are as follows:
Australopiths = 3.8 yr (median = 3.9, min = 3.2, max = 4.0);
Early *Homo* = 4.1 yr (median = 4.1, min = 3.9, max = 4.2);
Middle Pleistocene *Homo* = 5.1 yr (median = 4.9, min = 4.3, max = 6.9);
Late Pleistocene *Homo* = 7.3 yr (median = 7.5, min = 4.9, max = 10.1)

### Section 6.1.3.B Model Cubic-1C (Catarrhine, Extant)

In Chapter 5, the results showed that Model Cubic-1C (Catarrhine, Extant Only) meets stage one criteria: pred-$M_1$Age is within AC for *H. erectus, H. sapiens*, *P. troglodytes*, and *H. neanderthalensis*. However Cubic-1C pred-$M_1$Age is over-predicted above RC in Australopiths and Fossil *H. sapiens*.

Applied to all of the individual fossil hominin ECVs, Model Cubic-1C the average pred-$M_1$Age of the *Homo erectus* group = 4.3 yr (African *H. erectus* = 4.2 yr, East Asian *H. erectus* = 4.5 yr, Southeast Asian *H. erectus* = 4.3 yr). Average pred-$M_1$Age for the remaining groups are as follows: Australopiths = 3.8 yr; Early *Homo* = 4.1 yr; Middle Pleistocene = 5.1 yr; Late Pleistocene = 7.3 yr. As with the previous Cubic models, Cubic-1C pred-$M_1$Age is largely within RC for the *H. e. erectus* group, but is again very over-predicted in the Middle and Late Pleistocene groups.

In Figure 6.9, the *H. e. erectus* group pred-$M_1$Age range plots nearly entirely within *H. erectus* RC. The pred-$M_1$Age ranges for Middle and Late Pleistocene plot much more widely than the other three groups, especially when considering the relative ECV ranges of each group (see the reference Figure 6.1). Pred-$M_1$Age range in the upper half of the Late Pleistocene group is highly over-predicted well above the upper limit of *H. neanderthalensis* RC. Aside from the lowest outliers of *A. afarensis*, the Australopiths group is over-predicted above the Australopith RC.

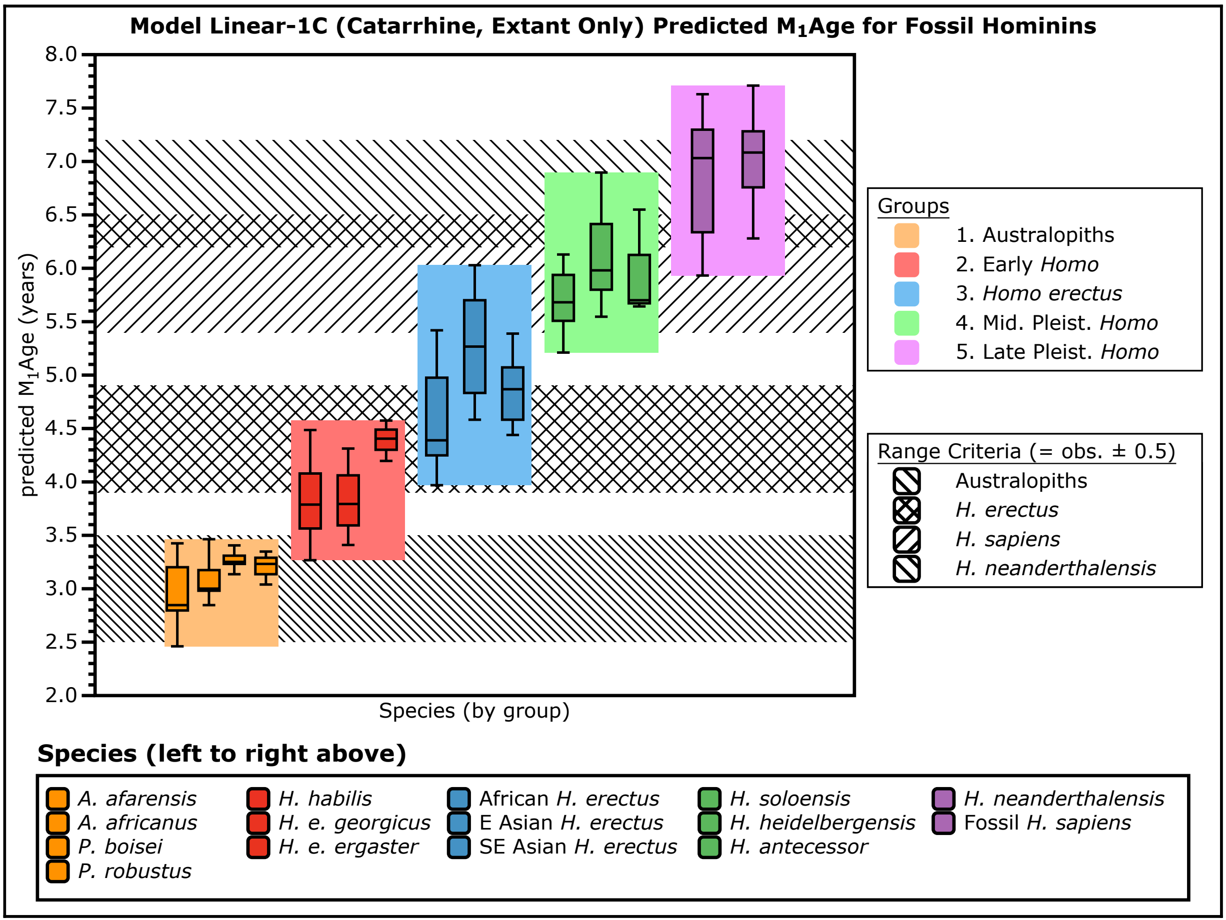

**Figure 6.10 Box & Whisker Plot: Linear-1C (Catarrhine, Extant Only)**
Model Linear-1C (Catarrhine, Extant Only) box plots, by species (grouped) of fossil hominin pred-M$_1$Age. Pred-M$_1$Age for the *H. e. erectus* group = 4.3 yr (median = 4.3 yr, 3.4—5.4). Pred-M$_1$Ages for the *H. e. erectus* regional subgroups are as follows: African *H. e. erectus* = 4.0 years; East Asian *H. e. erectus* = 4.7 years; Southeast Asian *H. e. erectus* = 4.2 years. Pred-M$_1$Age for the remaining groups are as follows: Australopiths = 2.5 years (median = 2.6, min = 1.9, max = 2.9); Early Homo = 3.3 years (median = 3.2, min = 2.7, max = 4.0); Middle Pleistocene *Homo* = 5.4 years (median = 5.3, min = 4.6, max = 6.3); Late Pleistocene *Homo* = 6.3 years (median = 6.5, min = 5.3, max = 7.1).

### Section 6.1.3.C Linear-1C (Catarrhine, Extant Only)

In Chapter 5, the results showed that Model Linear-1C (Catarrhine, Extant Only) does not meet the stage one criteria. Model Linear-1C (Catarrhine, Extant Only) predicts $M_1$Age within RC for *H. neanderthalensis,* but is outside of RC for the other fossil hominins.

When Model Linear-1C is applied to the fossil hominin ECV sample, the average pred-$M_1$Age for the *H. e. erectus* group = 5.4 yr (African *H. erectus*= 5.1 yr, East Asian *H. erectus*= 5.7 yr, Southeast Asian *H. erectus*= 5.3 yr). Pred-$M_1$Age for the remaining fossil hominin groups are as follows: the Australopiths = 3.6 yr; Early *Homo* = 4.5 yr; Middle Pleistocene = 6.2 yr; Late Pleistocene = 7.0 yr.

With Model Linear-1C, pred-$M_1$Age of the Late Pleistocene group falls largely within *H. sapiens* RC and *H. neanderthalensis* RC (combined). Pred-$M_1$Age of the Australopiths group fall largely in the lower half of RC or below RC. Pred-$M_1$Age in the *H. e. erectus* group ranges approximately 6 months above and below *H. erectus* RC.

### Summary

When comparing Figure 6.8 (ln-1C) with Figure 6.10 (Linear-1C), the upper limit of pred-$M_1$Age is similar, however a larger degree of pred-$M_1$Age appear to be predicted above RC in the ln-transformed model. Comparing Figure 6.8 (ln-1C) with Figure 6.2 (ln-1A) and Figure 6.5 (ln-1B): pred-$M_1$Age ranges for the groups in Model ln-1C appear to start at a smaller pred-$M_1$Age at most of the group minimums (with the exception of Australopiths), and the group ranges are slightly smaller than in the ln-transformed model for Group 1B (ln-1B). The expected range criteria across fossil species pred-$M_1$Ages is 2.5 yr to 7.2 yr (range 4.7): ln-1A = 3—11 yr (8), ln-1B is 2.8—8.2 (5.4), and ln-1C is 2.8—7.5 (4.7). Model ln-1C overall pred-$M_1$Age appears to be closer to the target upper and lower range, but lacks accuracy within that range. Like all the models, ln-1C does not predict with accuracy the differences in $M_1$Age between species with similar ECV and dissimilar $M_1$Age.

## Section 6.2 Set 2 Models (Extant & Extinct)

### Section 6.2.1 Group 2A (Primate, Extant & Extinct)

This section presents the Group 2A (Primate,Extant & Extinct) Models (ln-2A, Quad-2A, and Linear-2A) pred-$M_1$Age calculated from available fossil hominin ECVs. Each model is presented in sub-sections with a box and whisker plot. After the three models are presented, there is a brief comparison summary at the end of this section.

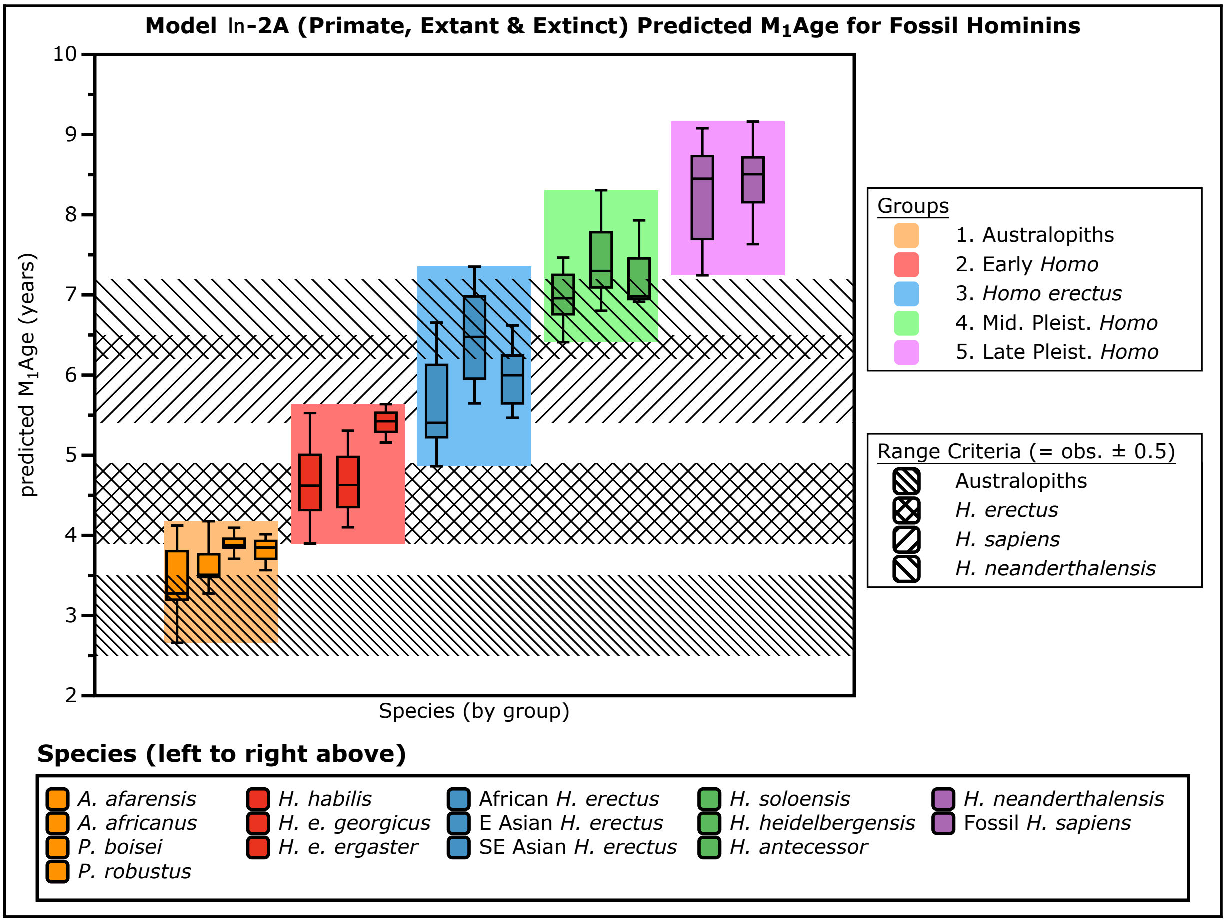

**Figure 6.11 Box & Whisker Plot: ln-2A (Primate,Extant & Extinct)**
Model ln-2A (Primate,Extant & Extinct) box plots of Fossil Hominin pred-$M_1$Age. Pred-$M_1$Age for the *H. e. erectus* group = 6.1 yr (median = 6.1, 4.9—7.4). Pred-$M_1$Age for the regional sub-groups as follows: African *H. erectus* = 5.7 yr; East Asian *H. erectus* = 6.5 yr; Southeast Asian *H. erectus* = 6.0 yr. Pred-$M_1$Ages for the remaining fossil hominin groups are as follows: Australopiths = 3.7 yr (median = 3.8, 2.7—4.2); Early *Homo* = 4.7 years (median = 4.7, 3.9—5.6); Middle Pleistocene *Homo* = 7.2 years (median = 7.2, 6.4—8.3); Late Pleistocene *Homo* = 8.4 years (median = 8.5, 7.2—9.2).

### Section 6.2.1.A ln-2A (Primate,Extant & Extinct)

Model ln-2A (Primate, Extant & Extinct) does not meet the stage one inclusion criteria. Model ln-2A (Primate,Extant & Extinct) does not predict $M_1$Age within RC or AC for any of the fossil hominins. Model ln-2A over predicts $M_1$Age for all fossil hominins.

When applied to individual fossil hominin ECVs, the average pred-$M_1$Age for the *H. e. erectus* group = 6.1 yr (African *H. erectus* = 5.7 yr, East Asian *H. erectus* = 6.5 yr, Southeast Asian *H. erectus* = 6.0 yr). The average pred-$M_1$Ages for the remaining fossil hominin groups are as follows: the Australopiths = 3.7 yr; Early *Homo* = 4.8 yr; Middle Pleistocene = 7.3 yr; Late Pleistocene = 8.4 yr. In Figure 6.11, the over-prediction of Middle and Late Pleistocene groups can be seen. Pred-$M_1$Age in the *H. e. erectus* group is over-predicted with a wide spread, all above *H. erectus* RC. Pred-$M_1$Age starts within RC for the Australopiths, but over-predicts into the lower *H. erectus* RC. Combined pred-$M_1$Age RCs range from 2.5 through 7.2 years, however ln-2A's maximum pred-$M_1$Age is over-predicted 2 years above the upper RC.

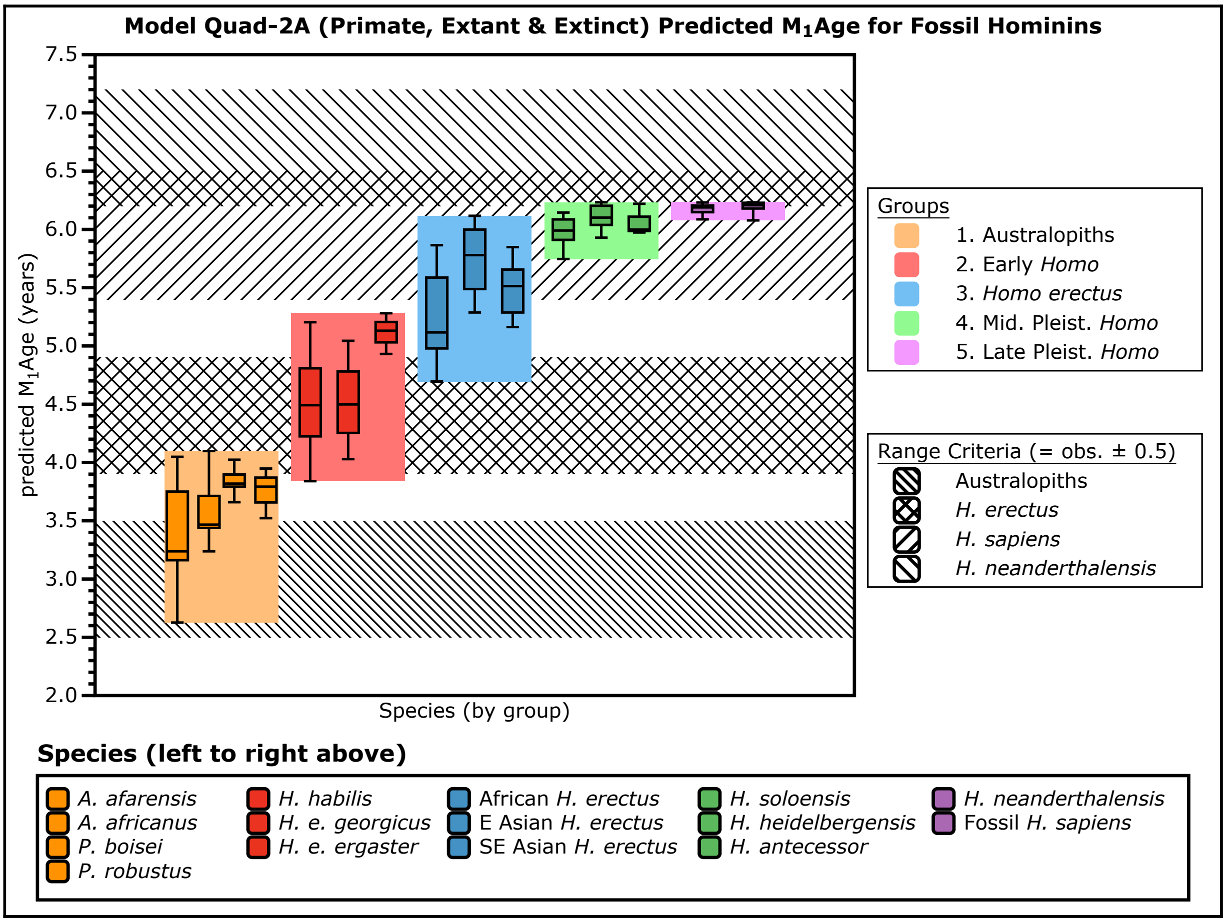

**FIGURE 6.12 BOX & WHISKER PLOT: QUAD-2A (PRIMATE,EXTANT & EXTINCT)**

Quad-2A (Primate,Extant & Extinct) box plots, by species (grouped) of fossil hominin pred-$M_1$Ages.

Pred-$M_1$Age for *H. e. erectus* = 5.5 yr (median = 5.9 yr, 4.7—6.1).

Pred-$M_1$Age for *H. e. erectus* sub-groups are:
African *H. e. erectus* = 5.3 yr;
East Asian *H. e. erectus* = 5.7 yr;
Southeast Asian *H. e. erectus* = 5.5 yr.
Pred-$M_1$Age for the remaining fossil hominins are as follows:
Australopiths = 3.6 yr (median = 4.3, 2.6—4.1);
Early *Homo* = 4.6 yr (median = 5.1, 3.8—5.3);
Middle Pleistocene *Homo* = 6.1 yr (median = 6.1, 5.7—6.2);
Late Pleistocene *Homo* = 6.2 yr (median = 5.4, 6.1—6.2).

### Section 6.2.1.B Quad-2A (Primate,Extant & Extinct)

Model Quad-2A (Primate, Extant & Extinct) does not meet the stage one inclusion criteria. Model Quad-2A predicts within RC for *H. neanderthalensis* and fossil *H. sapiens*, but does not predict $M_1$Age within AC for any fossil hominin. Model Quad-2A over predicts $M_1$Age for all other fossil hominins.

When applied to the fossil ECV sample, the mean of predicted $M_1$Age of the *Homo erectus* group = 5.5 yr (African *H. erectus* = 5.3 yr, East Asian *H. erectus* = 5.7 yr, Southeast Asian *H. erectus* = 5.5 yr). Pred-$M_1$Ages in the remaining groups are: the Australopiths = 3.6 yr; Early *Homo* = 4.6 yr; Middle Pleistocene = 6.1 yr; Late Pleistocene = 6.2 yr.

In Figure 6.12, there is a visibly compressed pred-$M_1$Age ranges in the Middle and Late Pleistocene groups. This contrasts with the wide pred-$M_1$Age ranges of the early hominin groups. The *H. e. erectus* group plots mostly above *H. erectus* RC. This model plots the upper range of East Asian H. e. erectus pred-$M_1$Age range with very little differentiation from the Middle and Late Pleistocene *Homo* pred-$M_1$Age ranges.

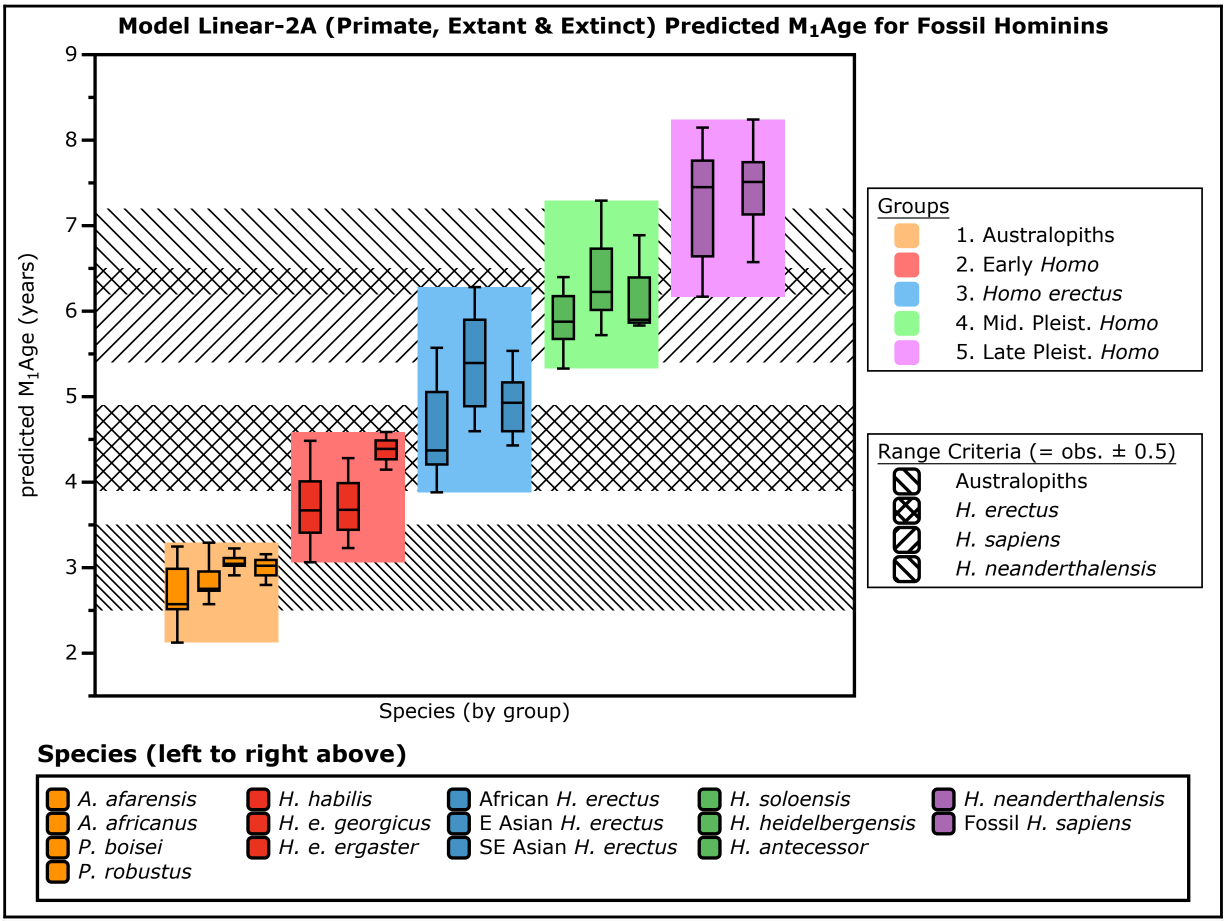

**Figure 6.13 Box & Whisker Plot: Linear-2A (Primate,Extant & Extinct)**

Linear-2A (Primate,Extant & Extinct) box plots, by species (grouped) for fossil hominin pred-$M_1$Ages.
Pred-$M_1$Age for *H. e. erectus* = 5.0 yr (median = 5.0 yr, 3.9—6.3).
Pred-$M_1$Age for *H. e. erectus* subgroups:
African *H. e. erectus* = 4.6 yr;
East Asian *H. e. erectus* = 5.4 yr;
Southeast Asian *H. e. erectus* = 4.9 yr.
Pred-$M_1$Age for the remaining fossil hominin groups:
Australopiths = 2.9 yr (median = 3.0, 2.1—3.3);
Early *Homo* = 3.8 yr (median = 3.7, 3.1—4.6);
Middle Pleistocene *Homo* = 6.2 yr (median = 6.1, 5.3—7.3);
Late Pleistocene *Homo* = 7.4 yr (median = 7.5, 6.2—8.2).

### Section 6.2.1.C   Linear-2A (Primate,Extant & Extinct)

Model Linear-2A (Primate, Extant & Extinct) does not meet the stage one inclusion criteria. Model Linear-2A (Primate,Extant & Extinct) predicts $M_1$Age within RC for the Australopiths, and also predicts within AC for the Australopiths. Model Linear-2A over predicts $M_1$Age for all other fossil hominins .

When applied to the fossil ECV sample, the mean of predicted M1Age of the *Homo erectus* group = 5.0 yr (median = 5.0; min = 3.9; max = 6.3). The mean of predicted $M_1$Ages for the *H. erectus* sub-groups are as follows: African *H. erectus* = 4.6 yr, East Asian *H. erectus* = 5.4 yr, Southeast Asian *H. erectus* = 4.9 yr.

The means of predicted $M_1$Age for the remaining groups are as follows: the Australopiths = 2.9 yr (median = 3.0, min = 2.1, max = 3.3); Early *Homo* = 3.8 yr (median = 3.7, min = 3.1, max = 4.6); Middle Pleistocene = 6.2 yr (median = 6.1, min = 5.3, max = 7.3). Late Pleistocene = 7.4 yr (median = 7.5, min = 6.2, max = 8.2). In Figure 6.13, both Late Pleistocene species plot within/above the *H. neanderthalensis* RC. *H. e. erectus* plots across both *H. erectus* RC and *H. sapiens* RC. The Australopiths plot mostly within RC.

### Section 6.2.2 Group 2B (Haplorhine, Extant & Extinct)

This section presents the Group 2B (Haplorhine, Extant & Extinct) Models ( $\ln$-2B, Quad-2B, and Linear-2B) pred-$M_1$Age calculated from available fossil hominin ECVs. Each model is presented in sub-sections with a box and whisker plot. After the three models are presented, there is a brief comparison summary at the end of this section.

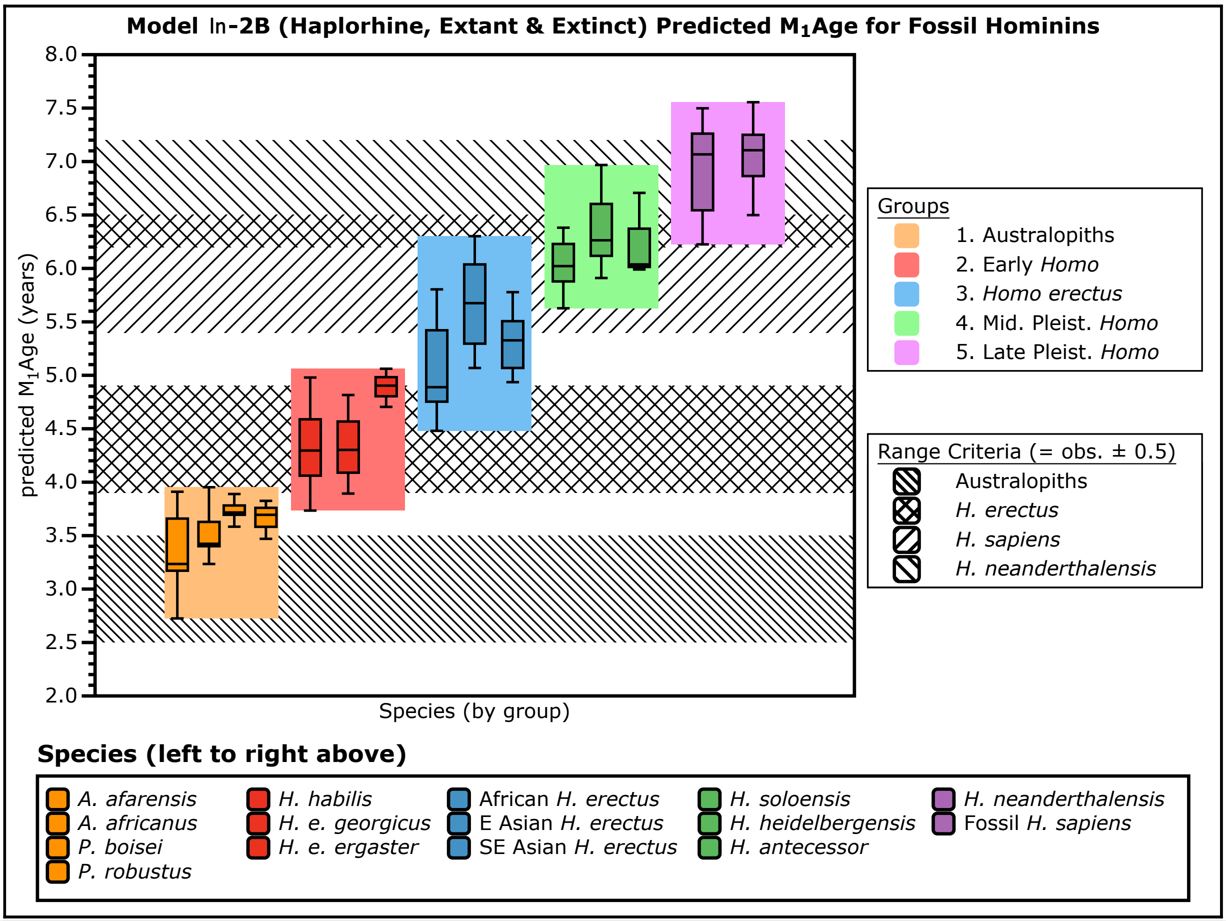

**FIGURE 6.14 BOX & WHISKER PLOT: ln-2B (HAPLORHINE, EXTANT & EXTINCT)**

ln-2B (Haplorhine, Extant & Extinct) box plots of Fossil Hominin predicted $M_1$Age.
Model ln-2B pred-$M_1$Age for *H. e. erectus* = 5.4 yr (median = 5.4 yr, 4.5—6.3).
Pred-$M_1$Age for *H. e. erectus* sub-groups are as follows:
African *H. erectus* = 5.1 yr;
East Asian *H. erectus* = 5.7 yr;
Southeast Asian *H. erectus* = 5.3 yr.
Pred-$M_1$Age for the remaining fossil hominin groups are as follows:
Australopiths = 3.6 yr (median = 3.6,2.7—4.0);
Early *Homo* = 4.3 yr (median = 4.3, 3.7—5.1);
Middle Pleistocene *Homo* = 6.2 yr (median = 6.2, 5.6—7.0);
Late Pleistocene *Homo* = 7.0 yr (median = 7.1, 6.2—7.6).

### Section 6.2.2.A ln-2B (Haplorhine, Extant & Extinct)

Model ln-2B (Haplorhine, Extant & Extinct) does not meet the stage one inclusion criteria. Model ln-2B only predicts $M_1$Age within RC for *H. neanderthalensis*. Model ln-2B over predicts $M_1$Age for all other fossil hominins.

When applied to the fossil ECV sample, the mean of predicted $M_1$Age of the *Homo erectus* group = 5.4 yr (median = 5.4; min = 4.5; max = 6.3). The mean of predicted $M_1$Ages for the *H. erectus* sub-groups are as follows: African *H. erectus* = 5.1 yr, East Asian *H. erectus* = 5.7 yr, Southeast Asian *H. erectus* = 5.3 yr. Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.6 yr; Early *Homo* = 4.4 yr; Middle Pleistocene = 6.3 yr; Late Pleistocene = 7.0 yr.

In Figure 6.14, the East Asian and the Southeast Asian *H. e. erectus* pred-$M_1$Age ranges plot above *H. erectus* RC. A large portion of the East Asian *H. e. erectus* pred-$M_1$Age range plots across most of the *H. sapiens* RC. Late Pleistocene pred-$M_1$Age plots both most of the range of species in the *H. neanderthalensis* RC. The pred-$M_1$Age range of two of the four Australopith species plot outside of the Australopith RC.

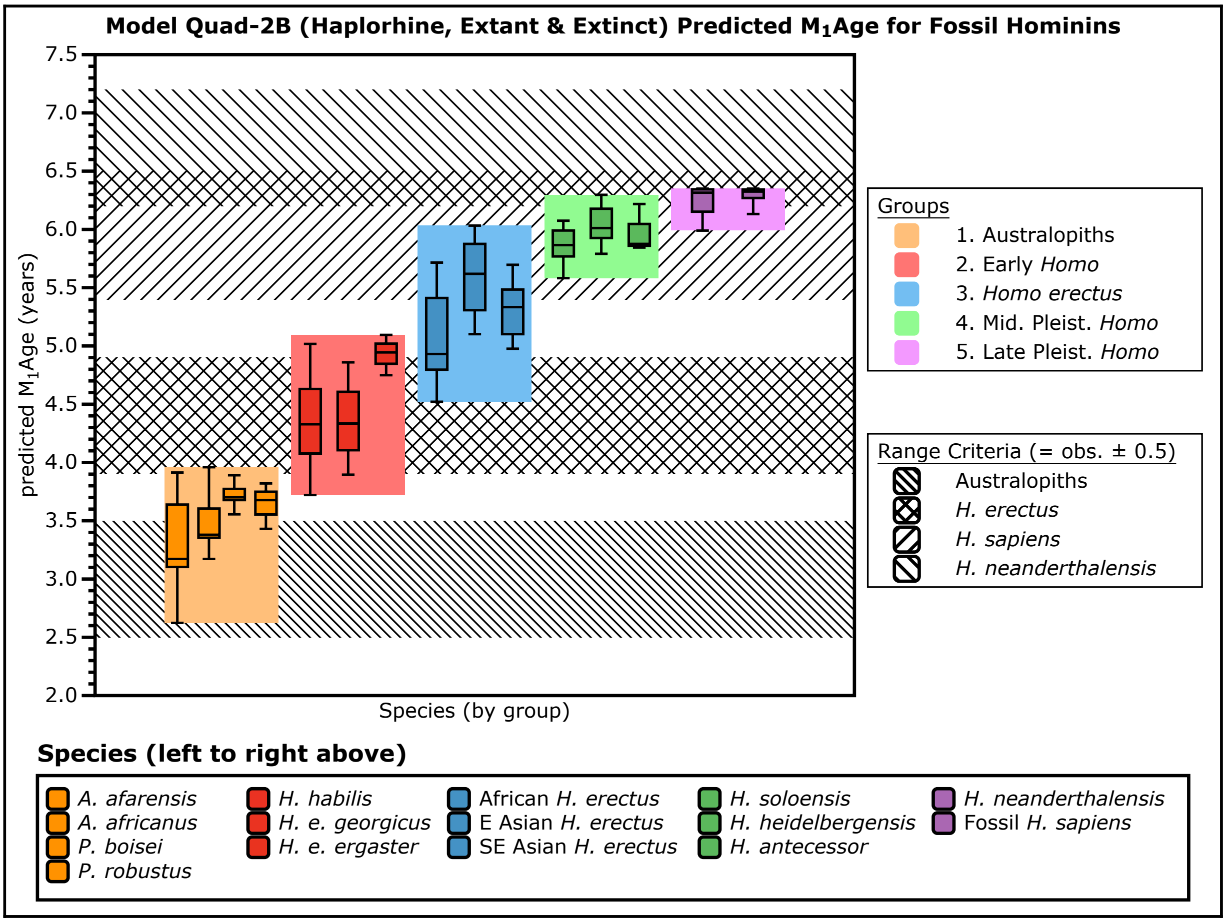

**Figure 6.15 Box & Whisker Plot: Quad-2B (Haplorhine, Extant & Extinct):**

Model Quad-2B (Haplorhine, Extant & Extinct) box plots of Fossil Hominin pred-$M_1$Age.
Pred-$M_1$Age for *H. e. erectus* = 5.4 yr (median = 5.4 yr, 4.5—6.0).
Pred-$M_1$Age for *H. erectus* sub-groups are as follows:
African *H. erectus* = 5.1 yr;
East Asian *H. erectus* = 5.6 yr;
Southeast Asian *H. erectus* = 5.3 yr.
Pred-$M_1$Age for the remaining fossil hominins are as follows:
Australopiths = 3.5 yr (median = 3.6, 2.6—4.0);
Early *Homo* = 4.5 yr (median = 4.4, 3.7—5.1);
Middle Pleistocene *Homo* = 6.0 yr (median = 6.0, 5.6—6.3);
Late Pleistocene *Homo* = 6.3 yr (median = 6.3, 6.0—6.4).

### Section 6.2.2.B Quad-2B (Haplorhine, Extant & Extinct)

Model Quad-2B (Haplorhine, Extant & Extinct) does not meet the stage one inclusion criteria. Model Quad-2B predicts within RC for *H. neanderthalensis* and fossil *H. sapiens*, and does not predict $M_1$Age within AC for any fossil hominin. Model Quad-2B over predicts $M_1$Age for all other fossil hominins.

When applied to the fossil ECV sample, the mean of predicted $M_1$Ages for the *Homo erectus* group = 5.4 yr (African *H. erectus* = 5.1 yr, East Asian *H. erectus* = 5.6 yr, Southeast Asian *H. erectus* = 5.3 yr). Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.5 yr; Early *Homo* = 4.5 yr; Middle Pleistocene = 6.0 yr; Late Pleistocene = 6.3 yr.

In Figure 6.15, *H. e. erectus* group's pred-$M_1$Age plots from the upper half of *H. erectus* RC through the lower half of *H. sapiens* RC. Middle and Late Pleistocene groups' pred-$M_1$Age ranges appear to abruptly cut off at the top end of the *H. sapiens* RC. The pred-$M_1$Age ranges of the early hominin and *H. erectus* groups plot more widely than the Middle and Late Pleistocene groups.

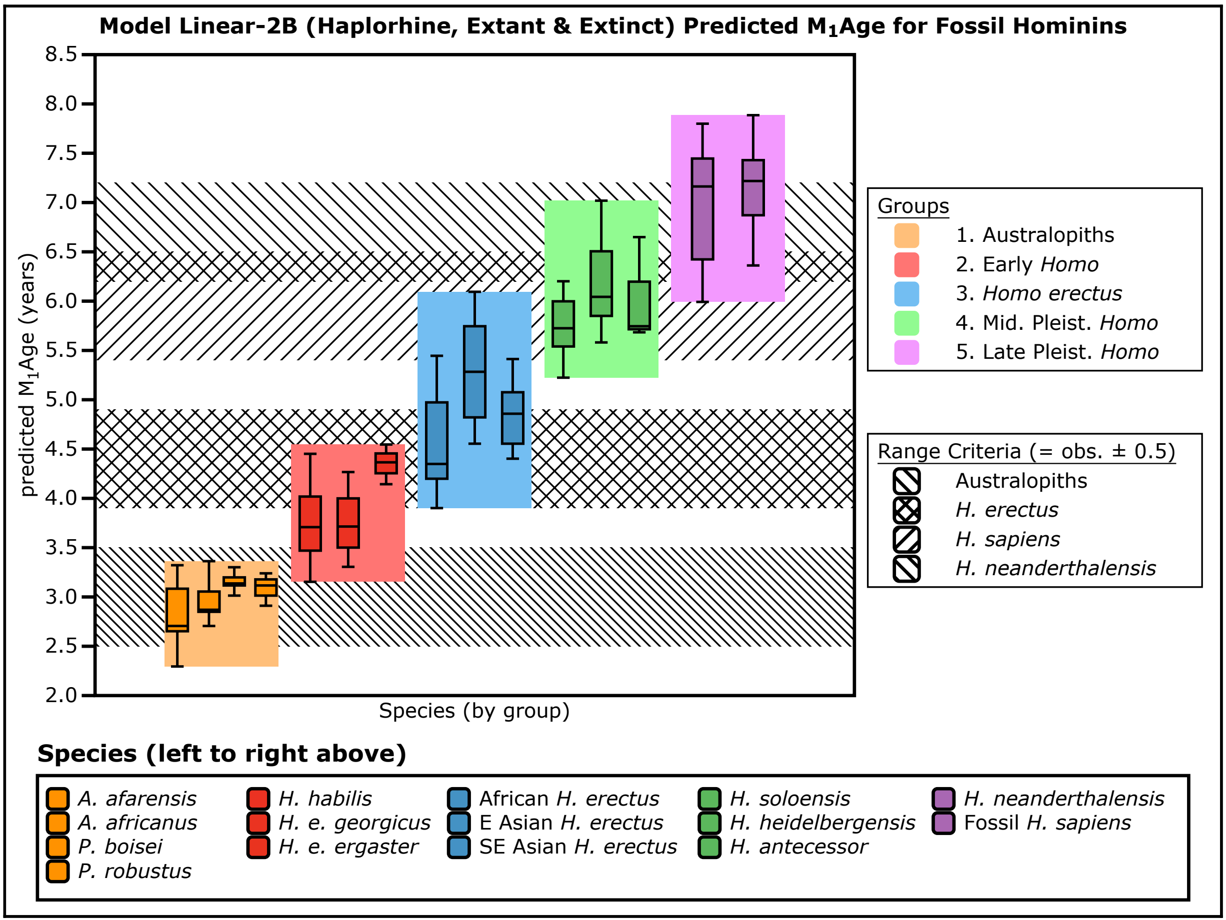

**FIGURE 6.16 BOX & WHISKER PLOT: LINEAR-2B (HAPLORHINE, EXTANT & EXTINCT)**
Model Linear-2B (Haplorhine, Extant & Extinct) box plots, by species (grouped) for fossil hominin pred-$M_1$Age ranges.
Pred-$M_1$Age for *H. e. erectus* = 4.9 yr (median = 4.9 yr, 3.9—6.1).
Pred-$M_1$Age for *H. e. erectus* sub-groups are as follows:
African *H. e. erectus* = 4.6 yr;
East Asian *H. e. erectus* = 5.3 yr;
Southeast Asian *H. e. erectus* = 4.8 yr.
Pred-$M_1$Age for the remaining fossil hominins are as follows:
Australopiths = 3.0 yr (median = 3.1, 2.3—3.4);
Early *Homo* = 3.9 yr (median = 3.7, 3.2—4.5);
Middle Pleistocene *Homo* = 6.0 yr (median = 5.9, 5.2—7.0);
Late Pleistocene *Homo* = 7.1 yr (median = 7.2, 6.0—7.9).

### Section 6.2.2.C Linear-2B (Haplorhine, Extant & Extinct)

Model Linear-2B (Haplorhine, Extant & Extinct) does not meet the stage one inclusion criteria. Model Linear-2B pred-$M_1$Age for *H. erectus* plots above AC. Pred-$M_1$Age is within AC only in the Australopiths.

When applied to the fossil ECV sample, the mean of predicted M1Age of the Homo erectus group = 4.9 years (African H. erectus= 4.6 years, East Asian H. erectus= 5.3 years, Southeast Asian H. erectus= 4.8 years). Pred-$M_1$Age for the remaining groups are as follows: the Australopiths = 3.0 years; Early Homo = 3.9 years; Middle Pleistocene = 6.0 years; Late Pleistocene = 7.1 years.

In Figure 6.16, the pred-$M_1$Age ranges for *H. e. erectus* and Middle & Late Pleistocene groups appear wider than the two early hominin groups. The pred-$M_1$Age ranges for the Late Pleistocene group plots mostly in or above the *H. neanderthalensis* RC. *H. e. erectus* plots across the *H. erectus* RC and most of the *H. sapiens* RC.

### Section 6.2.3 Group 2C (Catarrhine, Extant & Extinct)

This section presents the Group 2C (Catarrhine, Extant & Extinct) Models ( $\ln$-2C, Quad-2C, and Linear-2C) pred-$M_1$Ages calculated from available fossil hominin ECVs. Each model is presented in sub-sections with a box and whisker plot. After the three models are presented, there is a brief comparison summary at the end of this section.

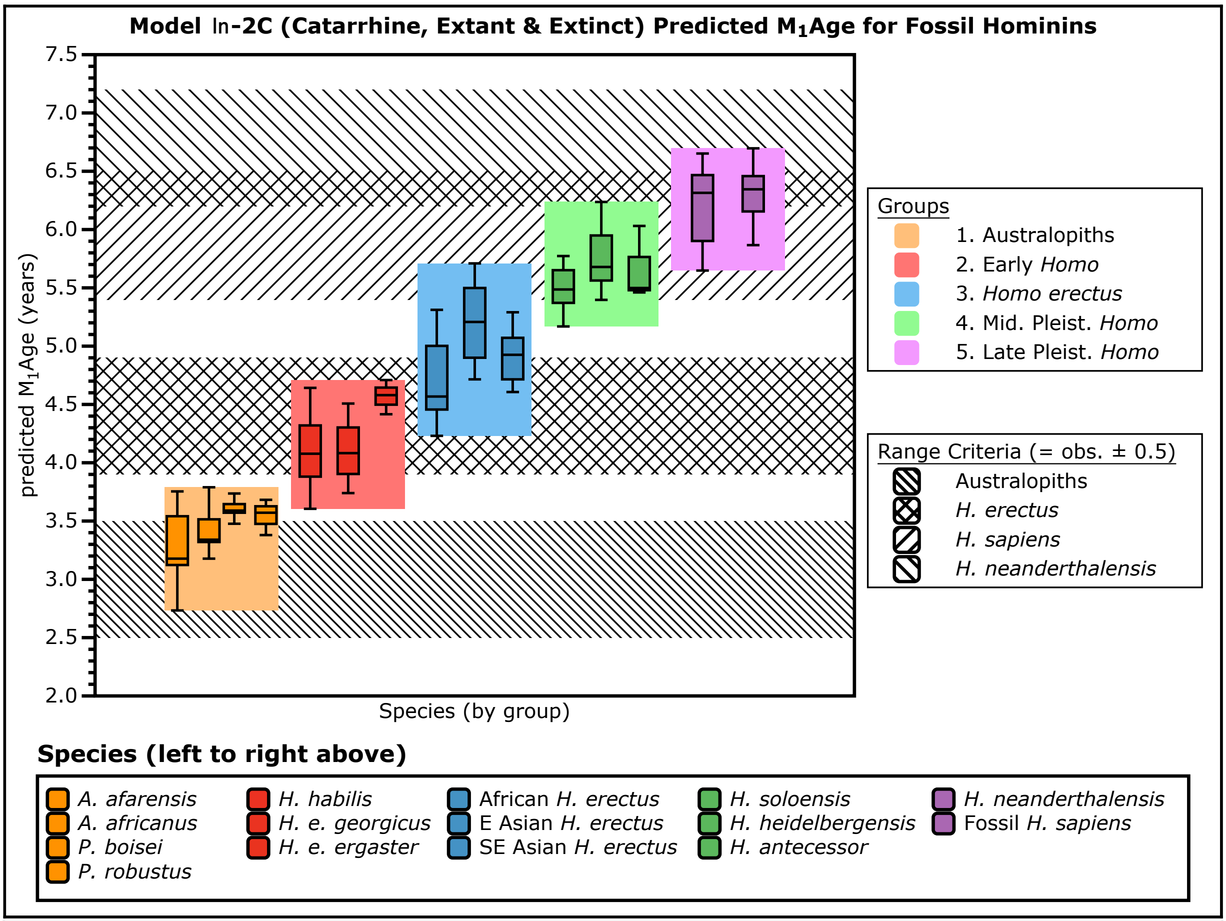

**FIGURE 6.17 BOX & WHISKER PLOT: ln-2C (CATARRHINE, EXTANT & EXTINCT)**

Model ln-2C (Catarrhine, Extant & Extinct) box plots of fossil hominin pred-$M_1$Age.
Model ln-2C pred-$M_1$Age for the *H. e. erectus* = 5.0 yr (median = 5.0 yr, 4.2—5.7).
Pred-$M_1$Age for *H. e. erectus* sub-groups as follows:
African *H. erectus* = 4.7 yr;
East Asian *H. erectus* = 5.2 yr;
Southeast Asian *H. erectus* = 4.9 yr.
Pred-$M_1$Age for the remaining fossil hominin groups are as follows:
Australopiths = 3.4 yr (median = 3.5,2.7—3.8);
Early *Homo* = 4.1 yr (median = 4.1, 3.6—4.7);
Middle Pleistocene *Homo* = 5.6 yr (median = 5.6, 5.2—6.2);
Late Pleistocene *Homo* = 6.3 yr (median = 6.3, 5.6—6.7).

## Section 6.2.3.A ln-2C (Catarrhine, Extant & Extinct)

Model ln-2C (Catarrhine, Extant & Extinct) does not meet the stage one inclusion criteria. Model ln-2C only predicts $M_1$Age within RC for *H. neanderthalensis* and fossil *H. sapiens*. Model ln-2C (Catarrhine, Extant & Extinct) over predicts $M_1$Age for all other fossil hominins.

When applied to the fossil ECV sample, the mean of predicted M1Age of the *Homo erectus* group = 5.0 yr (African *H. erectus*= 4.7 yr, East Asian *H. erectus*= 5.2.yr, Southeast Asian *H. erectus*= 4.9 yr). The means of predicted $M_1$Ages for the remaining groups are as follows: the Australopiths = 3.5 yr; Early *Homo* = 4.2 yr; Middle Pleistocene = 5.7 yr; Late Pleistocene = 6.3 yr.

In Figure 6.17, the *H. e. erectus* group plots across approximately 2/3 of the upper range of the *H. erectus* RC, up into the bottom half of the *H. sapiens* RC. The Late Pleistocene group straddles approximately the upper 3/4 of the *H. sapiens* RC through the lower half of the *H. neanderthalensis* RC. The Australopiths group plots in and above Australopith RC.

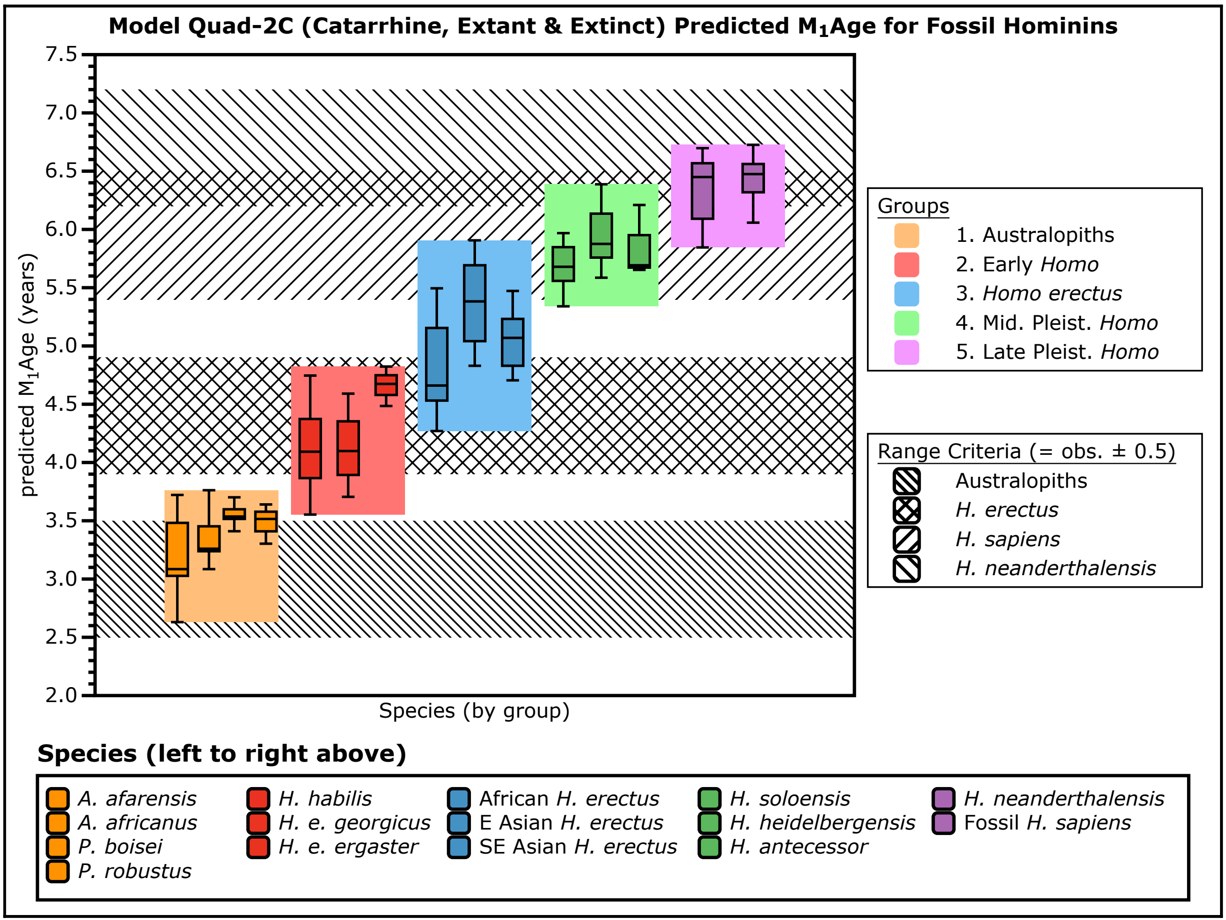

**FIGURE 6.18 BOX & WHISKER PLOT: QUAD-2C (CATARRHINE, EXTANT & EXTINCT)** Model Quad-2C (Catarrhine, Extant & Extinct) box plots of Fossil Hominin predicted $M_1$Age (years). Pred-M1Age for the *H. e. erectus* group = 4.7 yr (median = 5.1 yr, 4.3—5.9). Pred-$M_1$Age for *H. e. erectus* sub-groups are: African *H. erectus* = 4.5 yr; East Asian *H. erectus* = 5.0 yr; Southeast Asian *H. erectus* = 4.7 yr. Pred-$M_1$Age for the remaining fossil hominin groups are as follows: Australopiths = 3.3 yr (median = 3.5, 2.6—3.8); Early *Homo* = 4.0 yr (median = 4.1, 3.6—4.8); Middle Pleistocene *Homo* = 5.5 yr (median = 5.8, 5.3—6.4); Late Pleistocene *Homo* = 6.2 yr (median = 6.5, 5.8—6.7).

### Section 6.2.3.B Quad-2C (Catarrhine, Extant & Extinct)

Model Quad-2C (Catarrhine, Extant & Extinct) does not meet the stage one inclusion criteria. Model Quad-2C predicts $M_1$Age within RC for the Australopiths, and *H. neanderthalensis*, but does not predict $M_1$Age within AC for any fossil hominin. Model Quad-2C over predicts $M_1$Age for all other fossil hominins.

When Model Quad-2C (Catarrhine, Extant & Extinct) is applied to the fossil ECV sample, the mean of predicted $M_1$Ages of the *H. e. erectus* group = 4.7 yr (African *H. e. erectus* = 4.5 yr, East Asian *H. e. erectus* = 5.0 yr, Southeast Asian *H. e. erectus* = 4.7 yr). Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.3 yr; Early *Homo* = 4.0 yr; Middle Pleistocene = 5.5 yr; Late Pleistocene = 6.2 yr.

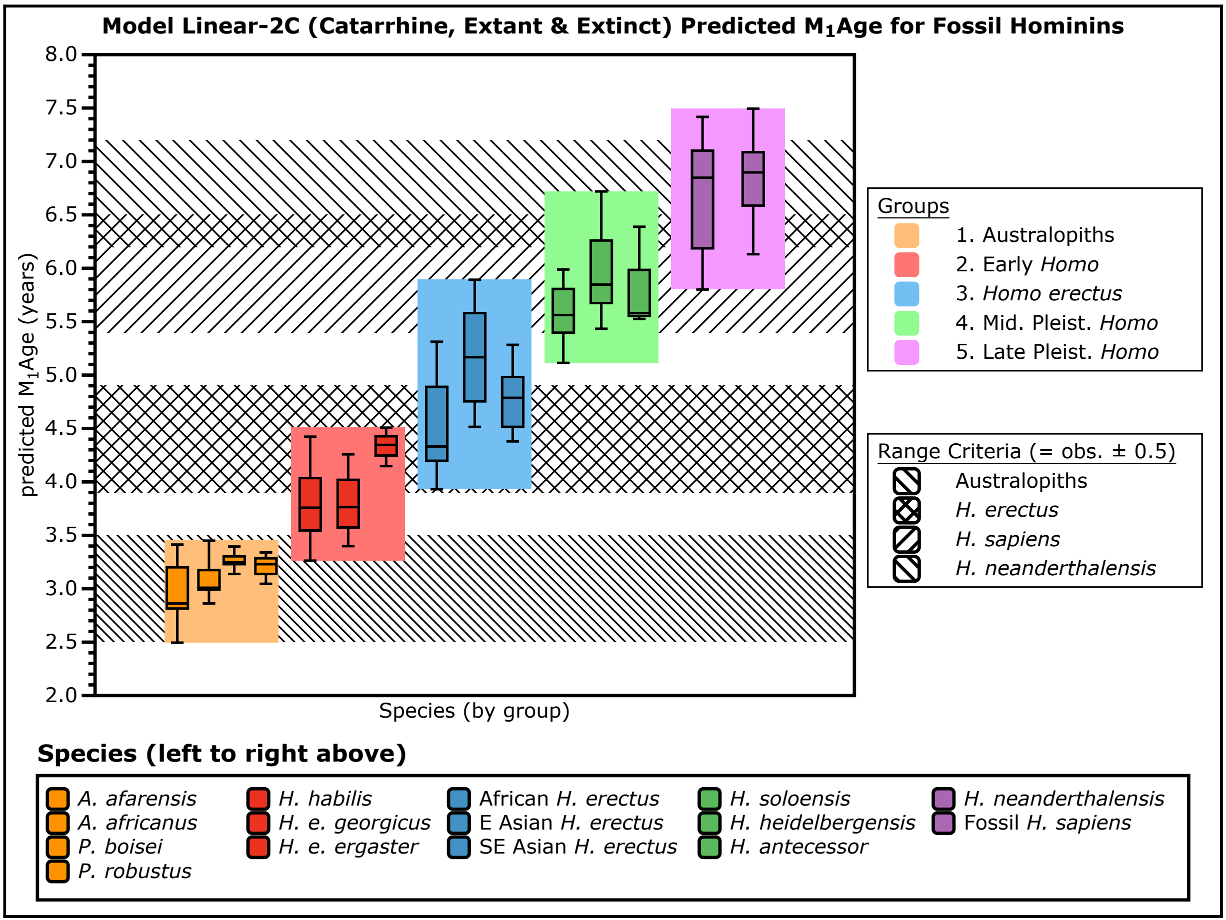

**Figure 6.19 Box & Whisker Plot: Linear-2C (Catarrhine, Extant & Extinct)**
Model Linear-2C (Catarrhine, Extant & Extinct) box plots, by species (grouped) of Fossil Hominin pred-M$_1$Age.
Pred-M$_1$Age for *H. e. erectus* group = 4.9 yr (median = 4.8 yr, 3.9—5.9).
Pred-M$_1$Ages for *H. e. erectus* regional sub-groups:
African *H. e. erectus* = 4.5 yr;
East Asian *H. e. erectus* = 5.2 yr;
Southeast Asian *H. e. erectus* = 4.8 yr.
Pred-M$_1$Age for the remaining fossil hominin groups:
Australopiths = 3.1 yr (median = 3.2, 2.5—3.5);
Early *Homo* = 3.9 yr (median = 3.8, 3.3—4.5);
Middle Pleistocene *Homo* = 5.8 yr (median = 5.7, 5.1—6.7);
Late Pleistocene *Homo* = 6.8 yr (median = 6.9, 5.8—7.5).

### Section 6.2.3.C Linear-2C (Catarrhine, Extant & Extinct)

Model Linear-2C (Catarrhine, Extant & Extinct) meets the stage one inclusion criteria. Model Linear-2C predicts $M_1$Ages within RC for the Australopiths, *H. erectus*, and *H. neanderthalensis*, and predicts within AC for the Australopiths and *H. neanderthalensis*. Model Linear-2C over predicts $M_1$Age for fossil *H. sapiens*.

When applied to the fossil ECV sample, the mean of predicted $M_1$Age of the *Homo erectus* group = 4.9 yr (African *H. erectus* = 4.5 yr, East Asian *H. erectus* = 5.2 yr, Southeast Asian *H. erectus* = 4.8 yr). The means of predicted $M_1$Ages for the remaining groups are as follows: the Australopiths = 3.1 yr; Early *Homo* = 3.9 yr; Middle Pleistocene = 5.8 yr; Late Pleistocene = 6.8 yr.

In Figure 6.19, *H. erectus* group plots very widely, across *H. erectus* RC and most of *H. sapiens* RC. The Australopith pred-$M_1$Ages, by contrast, appear to plot neatly within the Australopith RC.

## Section 6.2.4 Group 2D (Hominoids, Extinct Added)

This section presents the Group 2D (Hominoid, Extant & Extinct) Model ($\ln$-2D, Quad-2D, and Linear-2D) pred-$M_1$Ages calculated from available fossil hominin ECVs. Each model is presented in sub-sections with a box and whisker plot.

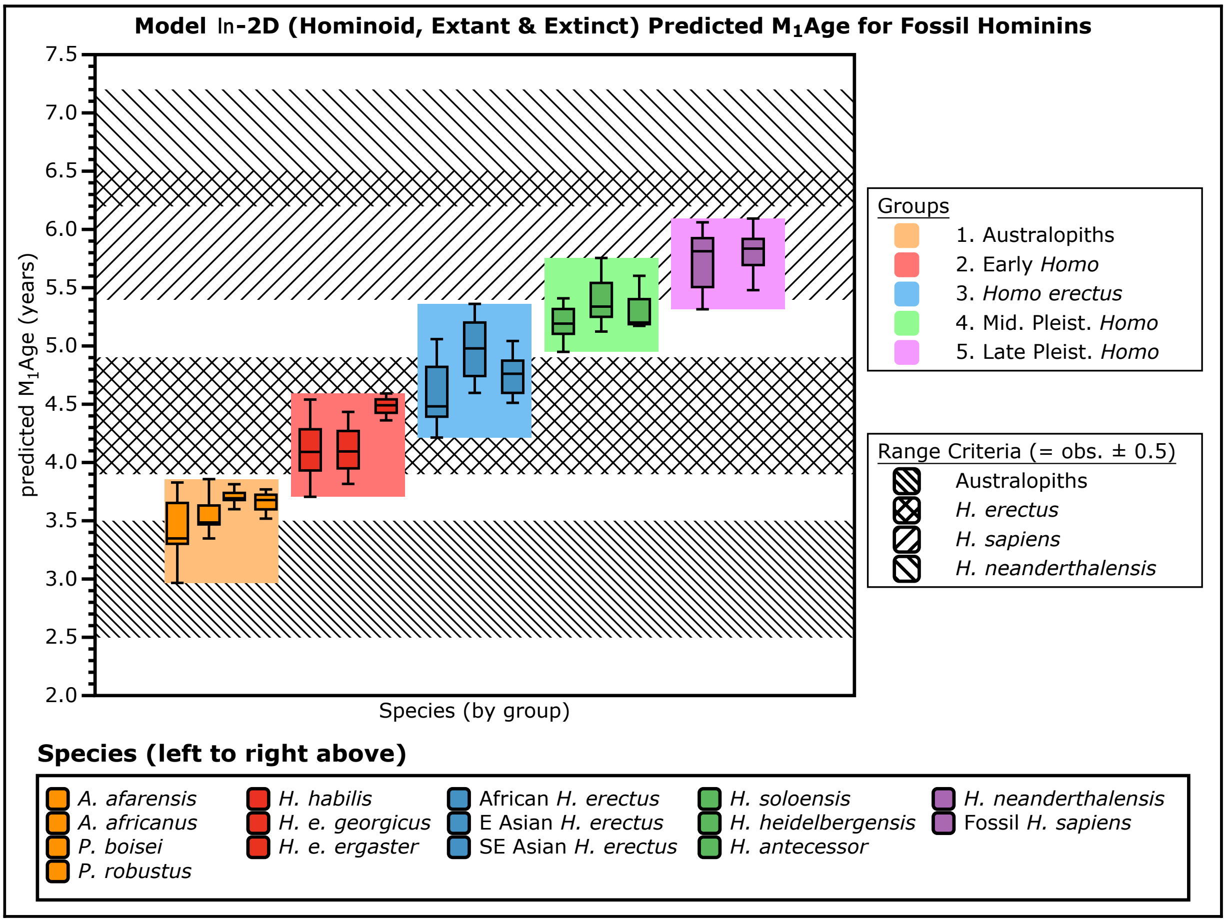

**FIGURE 6.20 BOX & WHISKER PLOT: ln-2D (HOMINOID, EXTANT & EXTINCT)**

Model ln-2D (Hominoid, Extant & Extinct) box plots, by species (grouped) for fossil hominin pred-$M_1$Age ranges.
Pred-$M_1$Age for the *H. e. erectus* = 4.8 yr (median = 4.8 yr, 4.2—5.4).
Pred-$M_1$Ages for *H. e. erectus* regional sub-groups are as follows:
African *H. erectus* = 4.6 yr;
East Asian *H. erectus* = 5.0 yr;
Southeast Asian *H. erectus* = 4.8 yr.
Pred-$M_1$Age for the remaining fossil hominins are as follows:
Australopiths = 3.6 yr (median = 3.6, 3.0—3.9);
Early *Homo* = 4.1 yr (median = 4.1, 3.7—4.6);
Middle Pleistocene *Homo* = 5.3 yr (median = 5.3, 4.9—5.8);
Late Pleistocene *Homo* = 5.8 yr (median = 5.8, 5.3—6.1).

### Section 6.2.4.A ln-2D (Hominoid, Extant & Extinct)

In Chapter 5, the results showed that Model ln-2D (Hominoid, Extant & Extinct) meets the stage one inclusion criteria. Pred-$M_1$Age is within RC for *H. erectus* and fossil *H. sapiens*, but is over-predicted for the other fossil hominins. When applied to individual fossil hominin ECVs, the average pred-$M_1$Age for *H. e. erectus* = 4.8 yr (African *H. e. erectus* = 4.6 yr, East Asian *H. e. erectus* = 5.0 yr, Southeast Asian *H. e. erectus* = 4.8 yr). Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.6 yr; Early *Homo* = 4.2 yr; Middle Pleistocene = 5.3 yr ; Late Pleistocene *Homo* = 5.8 yr.

In Figure 6.20, the compressed spread of pred-$M_1$Ages can be seen. There is not an over-prediction in the upper range of ECVs, but the range for Late Pleistocene *Homo* is low for *H. neanderthalensis*. Only around half of pred-$M_1$Age for the *H. e. erectus* group is within RC, the rest is over-predicted above RC, but is not so high as to be within *H. sapiens* RC. Australopith group pred-$M_1$Ages plot from within the upper half of Australopith RC or above.

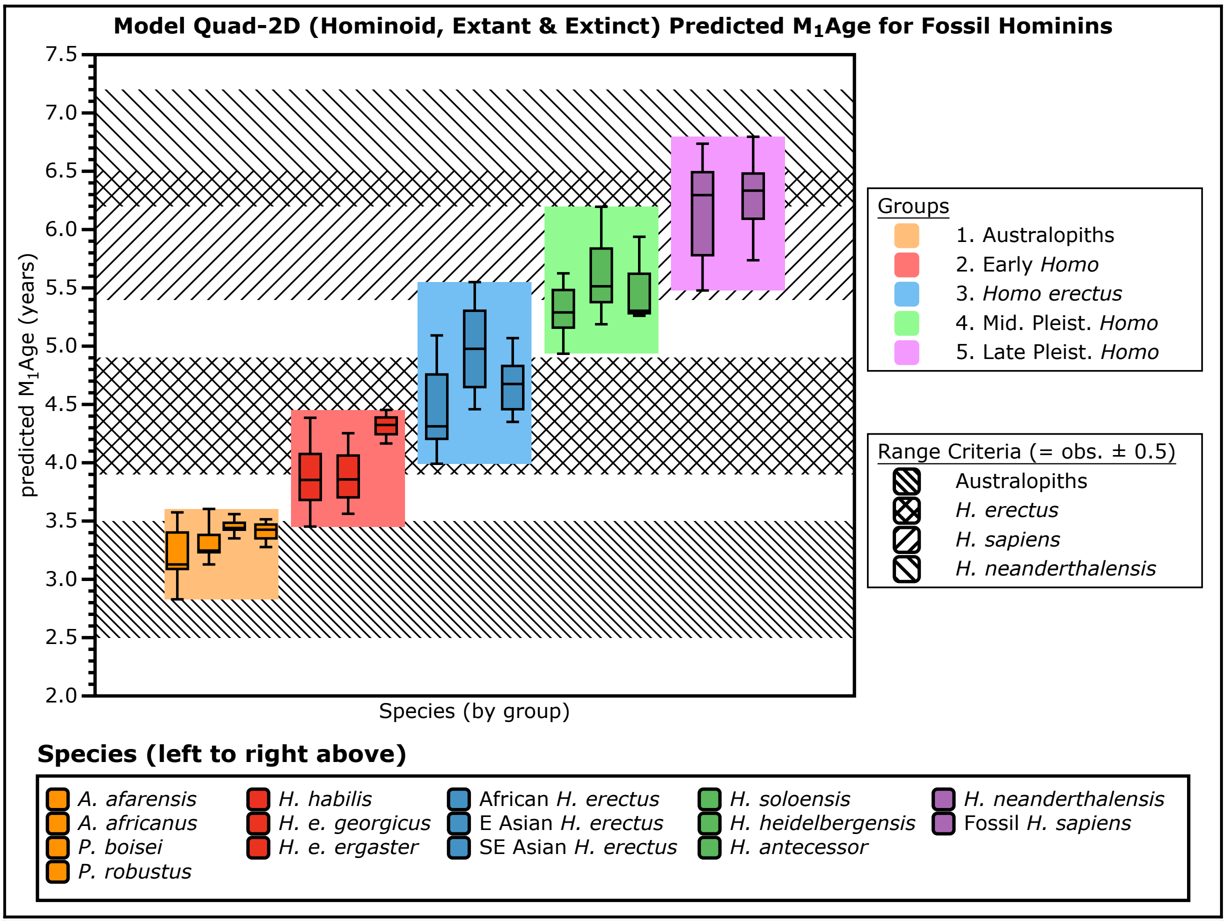

**FIGURE 6.21 BOX & WHISKER PLOT: QUAD-2D (HOMINOID, EXTANT & EXTINCT)**
Model Quad-2D (Hominoid, Extant & Extinct) box plots, by species (grouped), of Fossil Hominin pred-$M_1$Age ranges.
Pred-$M_1$Age for the *H. e. erectus* group = 4.7 yr (median = 4.7 yr, 4.0—5.5).
Pred-$M_1$Age for *H. e. erectus* sub-groups are as follows:
African *H. e. erectus* = 4.5 yr;
East Asian *H. e. erectus* = 5.0 yr;
Southeast Asian *H. e. erectus* = 4.7 yr.
Pred-$M_1$Age for the remaining fossil hominin groups:
Australopiths = 3.3 yr (median = 3.4, 2.8—3.6);
Early *Homo* = 4.0 yr (median = 3.9, 3.5—4.5);
Middle Pleistocene *Homo* = 5.5 yr (median = 5.4, 4.9—6.2);
Late Pleistocene *Homo* = 6.2 yr (median = 6.3, 5.5—6.8)

### Section 6.2.4.B Quad-2D (Hominoid, Extant & Extinct)

In Chapter 5, the results showed that Model Quad-2D meets the stage one criteria. Model Quad-2D pred-$M_1$Age is within RC for *H. erectus,* the Australopiths, *H. neanderthalensis*, and fossil *H. sapiens*, but is not within AC for any fossil hominin.

When applied to individual fossil hominin ECVs, the average pred-$M_1$Age in *H. e. erectus* group = 4.7 yr (African *H. erectus* = 4.5 yr, East Asian *H. erectus* = 5.0 yr, Southeast Asian *H. erectus* = 4.7 yr). Pred-$M_1$Ages for the remaining groups are as follows: the Australopiths = 3.3 yr; Early *Homo* = 4.0 yr; Middle Pleistocene = 5.5 yr; Late Pleistocene = 6.2 yr. In Figure 6.21, the *H. e. erectus* group plots across most of the *H. erectus* RC, and into the lowest edge of the *H. sapiens* RC.

In Figure 6.21, the *H. erectus* group plots across nearly all of the *H. erectus* RC and into the lower edge of the *H. sapiens* RC. The Late Pleistocene group plots across most of the *H. sapiens* RC and the lower half of the *H. neanderthalensis* RC. Most of the Australopiths group range plots within the Australopith RC and slightly above it.

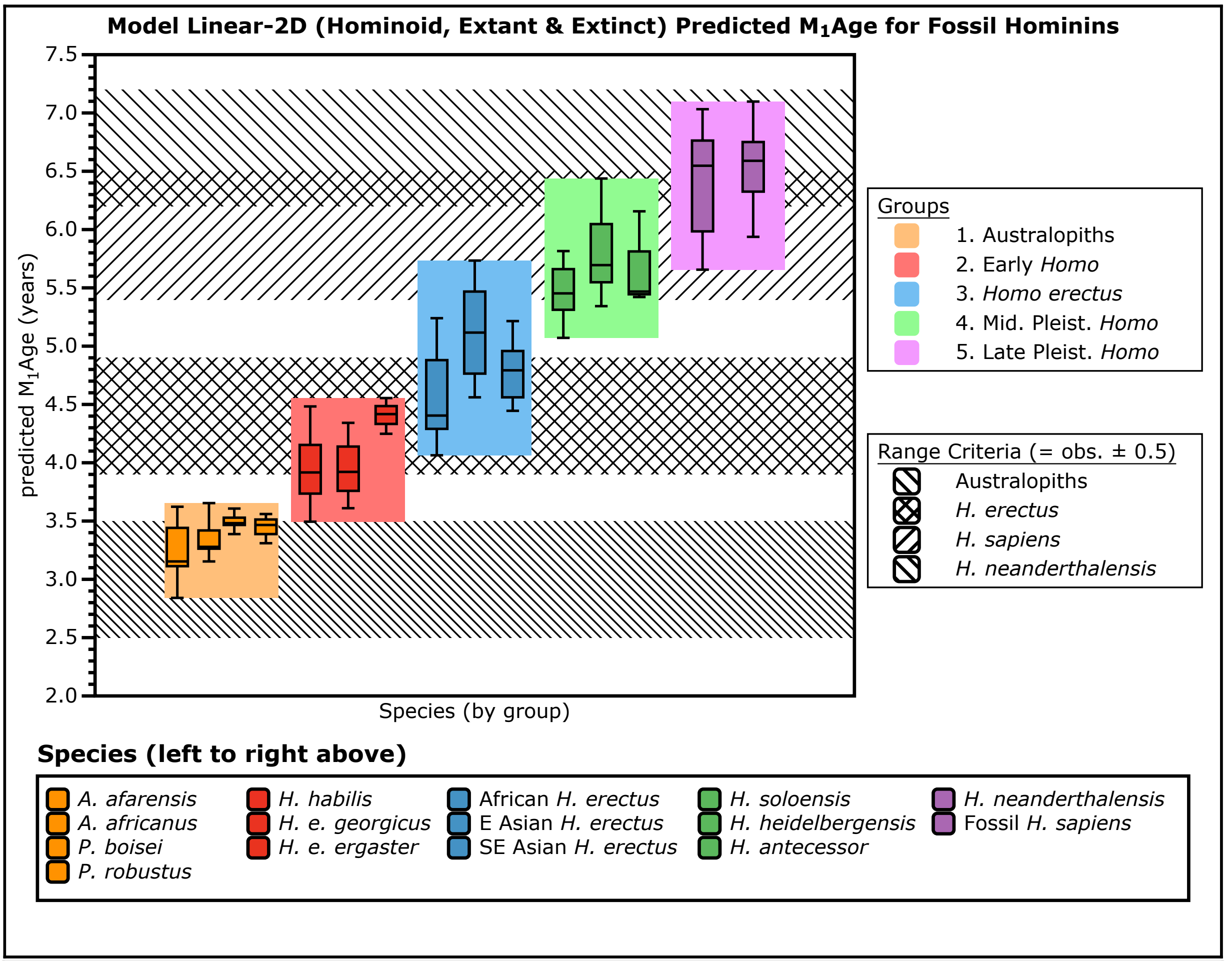

**FIGURE 6.22 BOX & WHISKER PLOT: LINEAR 2D (HOMINOID, EXTANT & EXTINCT)**
Model Linear-2D (Hominoid, Extant & Extinct) box plots, by species (grouped), of Fossil Hominin pred-$M_1$Age (years).
Pred-$M_1$Age for the *H. e. erectus* group = 4.9 yr (median = 4.8 yr, 4.1—5.7).
Pred-$M_1$Age for the *H. e. erectus* regional sub-groups are:
African *H. e. erectus* = 4.6 yr*;*
East Asian *H. e. erectus* = 5.1 yr;
Southeast Asian *H. e. erectus* = 4.8 yr.
Pred-$M_1$Age for the remaining fossil hominin groups:
Australopiths = 3.4 yr (median = 3.4, 2.8—3.7);
Early *Homo* = 4.0 yr (median = 3.9, 3.5—4.6);
Middle Pleistocene *Homo* = 5.7 yr (median = 5.6, 5.1—6.4);
Late Pleistocene *Homo* = 6.5 yr (median = 6.6, 5.7—7.1).

### Section 6.2.4.C Linear-2D (Hominoid, Extant & Extinct)

In Chapter 5, the results indicate that Model Linear-2D meets the stage one criteria. Pred-$M_1$Age is within RC for the Australopiths, *H. erectus,* and *H. neanderthalensis*, and over-predicted above RC for fossil *H. sapiens*. Linear-2D pred-$M_1$Ages are not within AC for any fossil hominin.

Applied to individual fossil hominin ECVs, the average of pred-$M_1$Age in *H. e. erectus* = 4.9 yr (African *H. erectus* = 4.6 yr, East Asian *H. erectus* = 5.1 yr, Southeast Asian *H. erectus* = 4.8 yr). Pred-$M_1$Ages in the remaining groups are as follows: the Australopiths = 3.4 yr; Early *Homo* = 4.0 yr; Middle Pleistocene = 5.7 yr. Late Pleistocene = 6.5 yr.

In Figure 6.22, it can be seen that *H. e. erectus* pred-$M_1$Age values are plotted across most of *H. erectus* RC and into the lower half of *H. sapiens* RC. The Australopiths are within to slightly over Australopith RC. Late Pleistocene *Homo* group plots within *H. sapiens* and *H. neanderthalensis* RCs.

### Section 6.2.5 Group 2E (Hominid, Extant & Extinct)

In Group 2E (Hominid, Extant & Extinct) only Quad-2E and Linear-2E passed first part of the stage one criteria. It is worth noting that Quad-2E has a reversed curve and a comparatively odd spread of pred-$M_1$Age ranges. Quad-2E and Linear-2E are discussed in sections below, followed by a brief comparison summary.

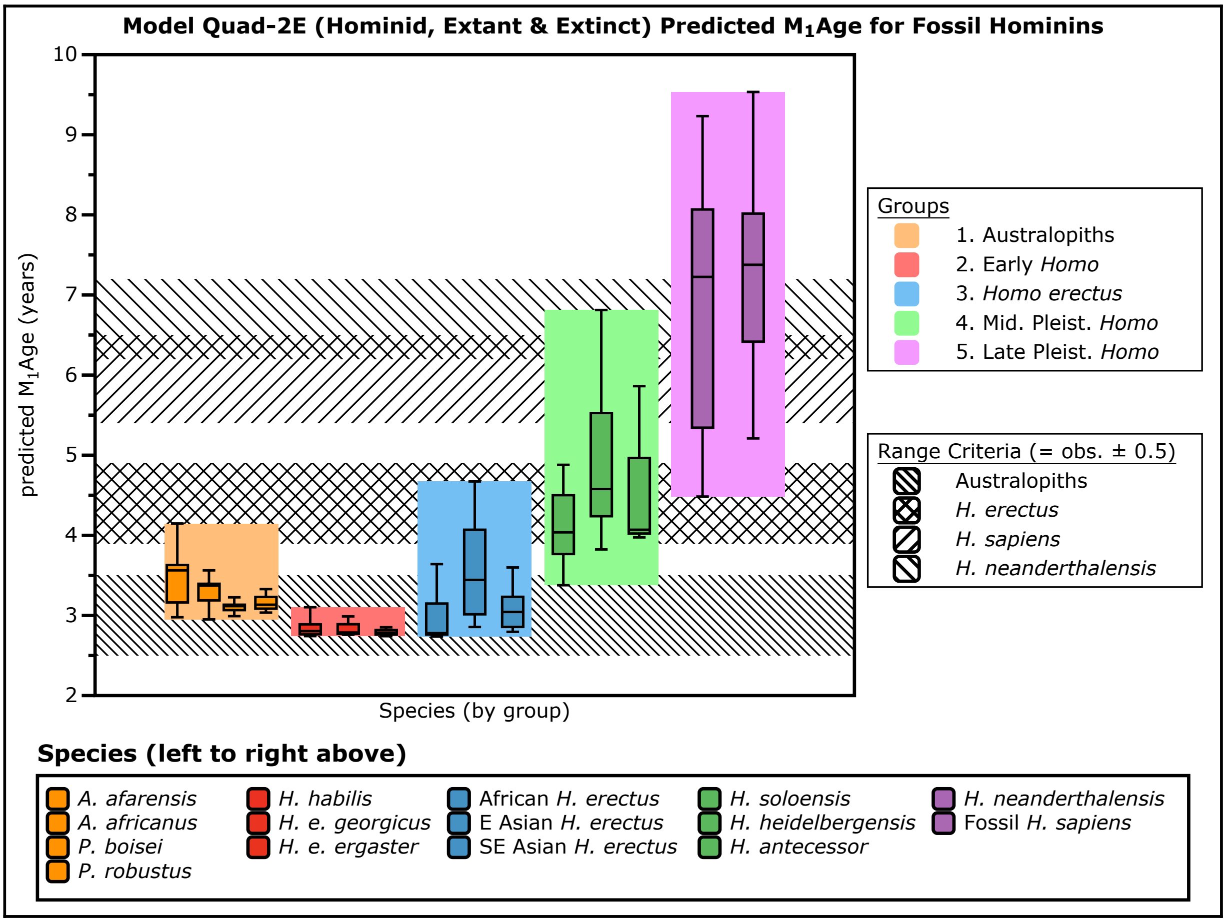

**Figure 6.23 Box & Whisker Plot: Quad 2D (Hominoid, Extant & Extinct)**

Quad-2D (Hominoid, Extant & Extinct) box plots, by species (grouped) of Fossil Hominin pred-M$_1$Age.

Pred-M$_1$Age in *H. e. erectus* group = 3.3 yr (median = 3.1 yr, 2.7—4.7).

Pred-M$_1$Age in the *H. e. erectus* regional subgroups is:
African *H. e. erectus* = 3.0 yr;
E Asian *H. e. erectus* = 3.6 yr;
SE Asian *H. e. erectus* = 3.1 yr.

Pred-M$_1$Age in the remaining fossil hominin groups is:
Australopiths = 3.3 yr (median = 3.2, 3.0—4.1);
Early *Homo* = 2.8 yr (median = 2.8, 2.7—3.1);
Middle Pleistocene *Homo* = 4.6 yr (median = 4.4, 3.4—6.8);
Late Pleistocene *Homo* = 7.1 yr (median = 7.4, 4.5—9.5)

### Section 6.2.5.A Quad-2E (Hominid, Extant & Extinct)

In Chapter 5, it is shown that Model Quad-2E does not meet stage one criteria. Pred-$M_1$Age is within RC for *H. sapiens, H. neanderthalensis*, and the Australopiths, but is outside RC for the other hominins. Applied to individual fossil hominin ECVs, the average of pred-$M_1$Age in *H. e. erectus* = 3.3 yr (African *H. erectus* = 3.0 yr; East Asian *H. erectus* = 3.6 years; SE Asian *H. erectus* =3.3 yr. Pred-$M_1$Age in the remaining fossil hominin groups:” Australopiths = 3.3 yr; Early *Homo* = 2.8 yr; Middle Pleistocene *Homo* = 4.6 yr; Late Pleistocene *Homo* = 7.1 yr.

In Figure 6.23, the effect of Quad-2E’s U-curve can be seen in the pred-$M_1$Age spreads. Australopith pred-$M_1$Age plots within the range of *H. e. erectus* group, and largely above African *H. e. erectus*. Pred-$M_1$Ages for Late Pleistocene group plot from below to well above combined *H. sapiens* and *H. neanderthalensis* RC.

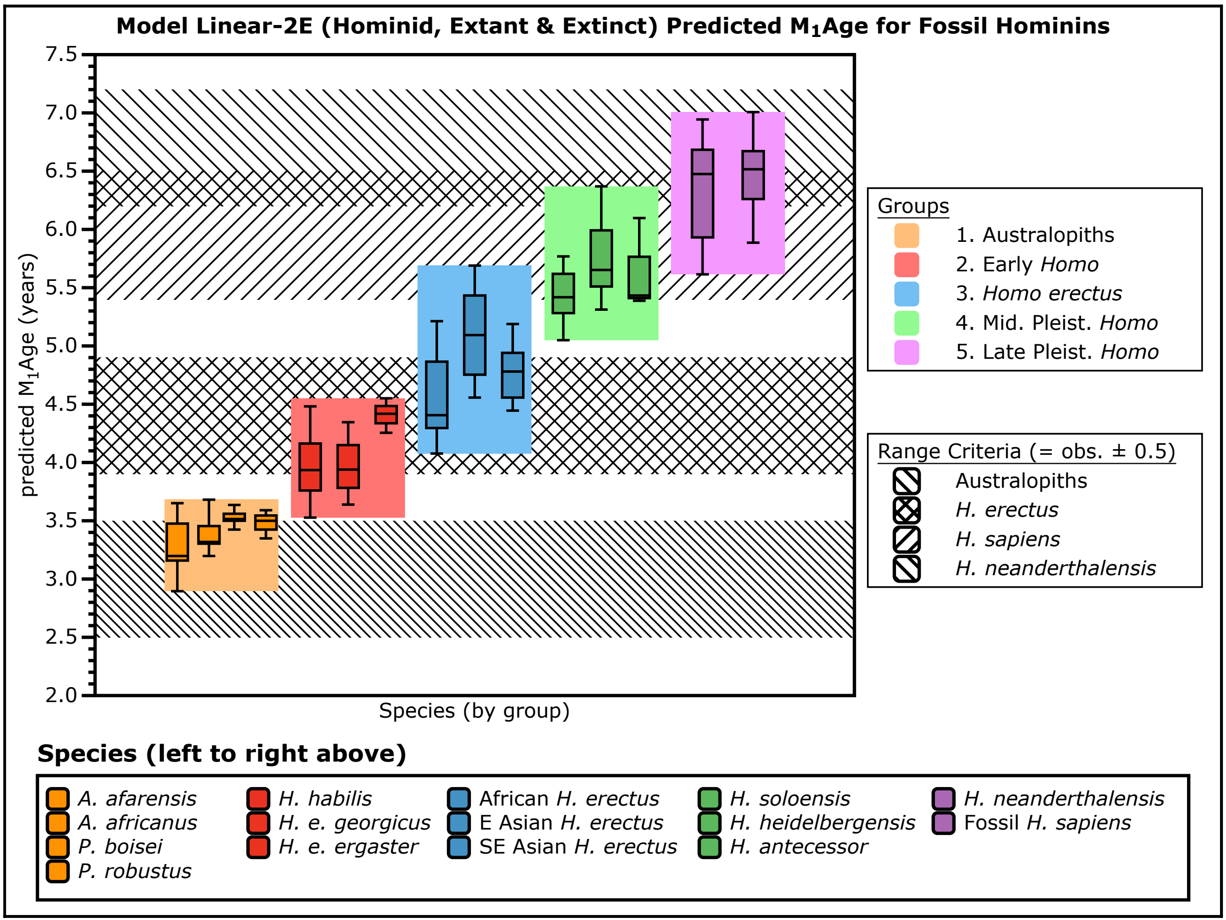

**Figure 6.24 Box & Whisker Plot: Linear-2E (Hominid, Extant & Extinct)**

Model Linear-2E (Hominid, Extant & Extinct) box plots, by species (grouped), of Fossil Hominin predM$_1$Age ranges.

Pred-M$_1$Age for the *H. e. erectus* group = 4.8 yr (median = 4.8 yr, 4.1—5.7).

Pred-M$_1$Ages for the *H. e. erectus* regional sub-groups:

African *H. e. erectus* = 4.6 yr;

East Asian *H. e. erectus* = 5.1 yr;

Southeast Asian *H. e. erectus* = 4.8 yr.

Pred-M$_1$Age for the remaining fossil hominin groups:

Australopiths = 3.4 yr (median = 3.5,2.9—3.7);

Early *Homo* = 4.1 yr (median = 4.0, 3.5—4.6);

Middle Pleistocene *Homo* = 5.6 yr (median = 5.6, 5.0—6.4);

Late Pleistocene *Homo* = 6.4 yr (median = 6.5, 5.6—7.0).

### Section 6.2.5.B Linear-2E (Hominid, Extant & Extinct)

In Chapter 5, it is shown that Model Linear-1A meets the stage one criteria. Pred-$M_1$Age is within RC for the *H. erectus,* H. neanderthalensis, and the Australopiths, and is over-predicted above RC for Fossil *H. sapiens*.

Applied to individual fossil hominin ECVs, the average pred-$M_1$Age in *H. e. erectus* = 5.2 yr (African *H. erectus*= 4.8 yr, East Asian *H. erectus*= 5.6 yr, Southeast Asian *H. erectus*= 5.1 yr). Pred-$M_1$Ages in the remaining groups are: the Australopiths = 3.0 yr; Early *Homo* = 4.0 yr; Middle Pleistocene = 6.5 yr; Late Pleistocene = 7.7 yr.

In Figure 6.24, is can be seen that pred-$M_1$Ages for the Late Pleistocene group fall within *H. sapiens* and *H. neanderthalensis* RCs. Again, like all the models, Fossil *H. sapiens* and *H. neanderthalensis* are not differentiated in pred-$M_1$Age ranges. *H. e. erectus* group plots from the lower half of *H. erectus* RC up to just into *H. sapiens* RC. Pred-$M_1$Ages for the Australopiths plot mostly within to slightly above RC.

## Summary

There are only two models which have *H. erectus* pred-$M_1$Age within AC without ad hoc adjustment: Cubic-1B (Haplorhine, Extant Only), and Cubic-1C (Catarrhine, Extant Only). Only one other fossil hominin test is within AC for those two models, and the others are over-predicted. Looking at the box plots for those models (Figure 6.6 and Figure 6.9) the extent to which they are not a good fit for the larger ECV ranges is clear, with such highly over-predicted values for the Late Pleistocene group.

Across all the Models, there is variation between which ranges are close to, within, outside of, or spread over multiple RCs. In some, minor changes in population selection for a mean ECV would not appear to result in different pred-$M_1$Age values. For instance, in Figure 6.15, any 2 populations from within either the *H. neanderthalensis* or Fossil *H. sapiens* hypodigms would plot very closely with each other. Meanwhile in other models population groups from each end of a larger hypodigm would return pred-$M_1$Ages which are differ by years. For instance for two populations from within *H. neanderthalensis* in Figure 6.3.

How one defines/splits paleo species when applying these models can bias pred-$M_1$Age values. Choosing the Asian *H. e. erectus* fossils to represent *H. erectus* will return an average ECV with a different pred-$M_1$Age than including the African fossils. The effect for *H. e. erectus* is much more pronounced in some models (such as Model ln-1A, Figure 6.2) than in others (such as Cubic-1C, Figure 6.6).

# Chapter 7

# Chapter 7 Discussion

This Chapter will discuss how the results presented above in Chapters 5 and 6 answer the questions of this thesis, before proceeding to a discussion of the issues raised by regressions and interpreting predictions for fossil hominins. This introduction will involve a brief review of the questions of the thesis. To answer if $M_1$Age/ECV regressions can be used to accurately predict hominin $M_1$Age, the question has been broken down into various parts:

- Does increasing/updating the number of species used (relative to previously published regressions) improve the predictions for *H. erectus*? i.e. is it the data set?
    - built with only extant primate data points (e.g. Model ln-1B)
    - built with the addition of fossil primate data points (Model ln-2B)
- When running the ln-transformed regressions on progressively taxonomically excluded subsets, are the predictions for *H. erectus* improved? (i.e. is it the specificity?)
    - relaxed criteria (e.g. Models ln-1A and ln-2A)
    - more restrictive criteria (e.g. Models ln-1C through ln-1E, and ln-2C, through ln-2E)
- Employing different equation types (e.g. Cubic, Quadratic, and Linear) to create equations: do any improve the prediction for *H. erectus*? i.e. is it the method? This will include all the steps above, with each equation type.

The first section of this chapter will first review where the results did or did not meet the accuracy criteria in stages based on the above questions. Throughout the first section, there will also be mention of accuracy for the other key fossil hominin species. The second section will discuss the issues that can arise when applying the prediction equations to fossil hominin specimen ECVs. The third section will discuss how issues with hominin fossil data impact the application of regression models and how predictions may impact the assessment of fossil hominin species, hominin taxonomies, and human life history evolution theories.

## Section 7.1 Increasing the Primate data set

The first step of the research was to compile an up-to-date list any published primate $M_1$Age data for which there was a published ECV for the species that could be paired with it. When first deciding to revisit $M_1$Age prediction, it was anticipated that, being many decades onwards, the size of the published data available for a Primate reference sample of $M_1$Age means would have increased. As presented above in the results chapters, I was able to moderately increase the size of the extant Primate data set. However, the increase was much less significant than originally had been anticipated.

The paucity of recorded $M_1$Age data for primates is likely an artefact of selection biases. For instance, laboratory research has recorded a considerable amount of data for *some* Primate species. Some species may also have received greater research coverage due to living in close proximity to humans, or in field-research-accessible environments. Aside from *P. troglodytes*, the large and longer-lived extant hominids have had less life history data recorded, based on fewer individuals. Thus more species can be included for the genus *Macaca* (n = 4) than can be included for the three genera of extant non-human hominids (n=3). Moreover, while the *Macaca* data points are calculated from larger sample sizes of $M_1$Age, *G. gorilla and P. pygmaeus* were included based on very tenuous sample sizes of estimated $M_1$Age (n = 2 and n = 1, respectively). These two hominids were included so that there would be more than one extant non-human hominid species included. Additionally, the observed $M_1$Age age for *H. erectus*, which was used to judge prediction accuracy, is derived from an estimated $M_1$Age of a single fossil individual.

Within the Extant Primate data set, there are instances in the extant Primate data where species at similar ECV have divergent $M_1$Age. With the three hominid species*, Pongo pygmaeus* has only a 12 ml larger ECV than *Pan troglodytes*, but a 1.5 year greater $M_1$Age. *G. gorillla* ECV 113 ml larger than *P. pygmaeus*, but *G. gorilla* $M_1$Age is intermediate to *P. pygmaeus* and *P. troglodytes*. Predicted $M_1$Age for these hominids is not within AC for all three in any of the 40 models generated.

The view of model accuracy can only be one of *apparent* accuracy based on both the sample size which creates the models, and the sample which is used to assess accuracy. So it is important to acknowledge how the available data limits this study’s assessment of “accuracy” to an exercise. That said, because of the limitations of currently available Primate $M_1$Age data, regressions are only likely to give us a general view of the overall pattern of the correlation of $M_1$Age to ECV, but not an accurate estimation of fossil hominin $M_1$Age. This will be seen repeatedly throughout the discussion of the method results.

## Section 7.2 The Models

The first step to assessing whether this type of life history regression equation makes a reasonably good fit for predicting fossil hominin $M_1$Age was to apply the regression model and exclusion criteria used in (Smith *et al.* 1995). Within this study, this corresponds to Model ln-1B (Haplorhine, Extant Only), which excludes strepsirrhines from the model. Following the tradition, Model ln-1B transforms both variables using ln ("natural" log or $\log_E$) before performing a least squares regression. Are the predictions accurate when the size of the primate reference sample is increased? Model ln-1B (Haplorhine, Extant Only) does not meet the primary criteria for inclusion without ad hoc adjustment of the predicted $M_1$Age for *H. erectus*.

So, increasing/updating the extant primate data set, does not, in itself, lead to accurate pred-$M_1$Age for *H. erectus* or the other fossil hominins. Options for interpretation of these results include some potential assumptions:

- These Pred-$M_1$Ages are actually correct and but the published $M_1$Ages estimates used to test them are incorrect:
  - *H. erectus* $M_1$Age is within the modern *H. sapiens* range
  - And all fossil hominin $M_1$Age estimates have been miscalculated

    - The recorded modern *H. sapiens* $M_1$Age data is also incorrect
- *Ha*-$M_1$Ages are correct and only the published $M_1$Age estimates for *H. erectus* and *H. neanderthalensis* are incorrect:
    - Australopiths vary from the line of regression in the same way that *H. sapiens* does, and this has a non-random cause:
        - Australopiths share a "grade" with modern *H. sapiens*
        - no other fossil hominins share a "grade" shift with modern *H. sapiens*
    - Fossil *H. sapiens* had a different $M_1$Age than modern *H. sapiens*
- Pred-$M_1$Age from Model ln-1B are inaccurate and $M_1$Age predictions from this regression should not be considered accurate estimates of $M_1$Age

It has been previously suggested that one possible interpretation of haplorhine $M_1$Age/ECV regression results which are not in agreement with published fossil hominin $M_1$Age estimates[35] is that those estimates could be incorrect (Kelley & Schwartz 2012). They also noted, however, the large 95% prediction intervals in $M_1$Age/ECV regressions. Given that in Model ln-1B 54% of the species used to create the model are not accurately predicted by the model, it is more likely that $M_1$Age/ECV regression model pred-$M_1$Age is not a reliable tool for calculating fossil hominin $M_1$Age. If pred-$M_1$Ages *are* treated as correct estimates of $M_1$Age for fossil hominins, then all published $M_1$Age estimates have

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[35] e.g. AgeAtDeath/$M_1$Age estimates for juvenile fossil hominins calculated from fossil tooth histology

been miscalculated. However, by this metric, there would also be a need to revisit the $M_1$Ages recorded for 13 extant primate species, including *H. sapiens*.

In the second scenario, *H*a-$M_1$Ages are accepted as accurate. Only a fossil hominin $M_1$Age which is not in agreement with the *H*a-$M_1$Age is then considered incorrect. Alternatively published $M_1$Age estimates which are not in agreement with *H*a-$M_1$Age are correct, but that species doesn’t vary from the Haplorhine regression line in the same way as *H. sapiens* does (if variation from the line of regression is assumed to be non-random). It would be important to remember that this regression violates other basic “assumptions” (such as normal distribution) while also relying on a limited sample number of observations pooled from non-matching populations. It seems more likely that variations from the line of regression are caused by the regression, and are not necessarily representative of biological variation from the line.

Which brings us to the third scenario: for Model ln-1B, pred-$M_1$Age is *not* an accurate estimate of $M_1$Age. The model lacks precision for the species with which the model is built. Issues with the application of predictions to the interpretation fossil hominin traits have been raised where regression models demonstrates large prediction errors for the primate species used to build the model (Smith 1996). Model ln-1B demonstrates a maximum absolute prediction error of 44%. Model ln-1B pred-$M_1$Age for *H. sapiens* is over-predicted by more than 16 months, while *P. pygmaeus* is under-predicted by the same amount. In model ln-1B, 54% of the pred-$M_1$Ages for extant Primates are predicted outside AC.

ln-1B pred-$M_1$Age is not within AC for *H. erectus,* and demonstrated a very wide spread of pred-$M_1$Ages within the larger ECV fossils. It is most probably that the regression model itself is inaccurate, and therefore that it is inappropriate to treat pred-$M_1$Age from extant Haplorhine ln-transformed models as an accurate estimate of $M_1$Age in fossil hominins. Is this lack of precision in fossil hominin pred-$M_1$Age unique to this specific taxonomic criteria (Haplorhine, Extant Only)?

### Section 7.2.1 Increasing the primate reference sample with histological $M_1$Age fossil Primate data

In this study, the Set 2 Models add fossil primate data points to the extant data set. This is done based on accepting published fossil hominin $M_1$Age estimates[36] as correct for this exercise. Model ln-2B (Haplorhine, Extant & Extinct) uses the same criteria as the model above, but with fossil data points added. In Chapter 5, the results showed that Model ln-2B produces pred-$M_1$Age for *H. erectus* (5.4 yr) which is outside of RC. Applying the *H*-residual produces an *Ha*-$M_1$Age for *H. erectus* (4.7 yr) within RC but AC. Applying the *P*-residual produces a *Pa*-$M_1$Age for *H. erectus* (5.5 yr) which is outside of RC.

Model ln-2B (Haplorhine, Extant & Extinct) predicted $M_1$Ages were inaccurate in 57% of the species used to build the model. The absolute % prediction error in Model ln-2B is 77.8%. Increasing the size of the Haplorhine data set by adding fossil data points, in itself, does not produce pred-$M_1$Ages

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[36] Again, this excludes the *H. erectus* $M_1$Age estimate, which is being used to test whether a hypothetical fossil hominin species, which is not included in the model (i.e. because there is not available $M_1$Age estimate available) can be accurately estimated through pred-$M_1$Age.

which are accurate for fossil hominins. Is the inaccuracy restricted to the Haplorhine criteria data sets alone?

## Section 7.2.2 Relaxed taxonomic restriction

The Group A (Primate) models are “less-restricted” (i.e. did not exclude the Strepsirrhine data points from the Primate data set as the Haplorhine models do). As a reminder, Group A has two data sets, 1A (Primate, Extant Only) and 2A (Primate,Extant & Extinct), and currently only the ln-transformed models are being discussed in this section (ln-1A and ln-2A). Is pred-$M_1$Age accurate for *H. erectus* and fossil hominins when all of the extant Primate data points are included? Model ln-1A (Primate, Extant Only) pred-$M_1$Age for *H. erectus* (7.1 yr) is over-predicted outside of RC, and is over-predicted for *H. erectus* in comparison to ln-1B pred-$M_1$Age by and additional 16 months.

The *H*a-$M_1$Age for *H. erectus* (4.5 yr) is within the primary and secondary criteria range. So, if the variation of *H. sapiens* from the Primate line of regression is accepted to be non-random, and *H. erectus* is assumed to vary from the line in the same way, then ln-1B *H*a-$M_1$Age can be viewed as accurate in *H. erectus*. More of Model ln-1A pred-$M_1$Ages are accurate for the species used to create it (64%), but it should be noted that no pred-$M_1$Ages are accurate in the hominids. ln-1A pred-$M_1$Age is not accurate for any fossil hominins, and ln-1A *H*a-$M_1$Age is not accurate in any fossil hominin aside from *H. erectus*.

With fossil specimens added, Model ln-2A (Primate, Extant & Extinct) also over-predicts all fossil hominins. When adjusted with the Model ln-2A *H. sapiens*-

residual, *H. erectus* is the only accurate fossil hominin value. Less of the model building species predicted $M_1$Ages are accurate in Model ln-2A than Model ln-1A. Most of these are still in the lower ECV range. The largest absolute percentage of error for species used in building ln-2A is 119%.

Both ln-1A and ln-2A over-predict for *H. erectus* by more than the above Model ln-1B and Model ln-2B. Including all Primate data points does not appear to improve prediction of fossil hominin $M_1$Age. The next section discusses the accuracy of, instead, increasing the amount of taxonomic exclusion (e.g. models C, D, and E).

### Section 7.2.3 Progressive taxonomic exclusion

Group B (Haplorhine) models, the starting point, leave out Strepsirrhine species. This section focuses on leaving out more species in an attempt to improve the fit of models. Does excluding more species models reduce the residuals? This section covers models ln-1C (Catarrhine, Extant Only) and ln-2C (Catarrhine, Extant & Extinct) and ln-2D (Hominoid, Extant & Extinct) in two parts, starting with the Set 1 model.[37]

#### Section 7.2.3.A Set 1

Model ln-1C (Catarrhine, Extant Only) has a reduced residual for *H. erectus,* in comparison to ln-1B. However, the ln-1C pred-$M_1$Age is still well over RC, and only predicts *H. neanderthalensis* within RC. No ln-1C pred-$M_1$Age is accurate in

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[37] Models ln-1D (Hominoid, Extant Only), ln-1E (Hominid, Extant Only), and ln-2E (Hominid, Extant & Extinct) are excluded from further discussion here because they did not pass the stage one test criteria outlined in Chapter 4 (Data & Regression Methods).

any fossil hominins. Model ln-1C is still inaccurate for 65% of the species used to create the model. *P. troglodytes* is the only hominid with pred-$M_1$Age within AC. Applying the *H*-residual or *P*-residual did not make the ln-1C *H. erectus* prediction come within accuracy. Within Set 1, restriction to Hominoids (Group D) or Hominids (Group E) left the models with small data sets ($n < 8$) and presumably this left too few data points to work with the regression model, and they did not pass initial criteria.

### Section 7.2.3.B Set 2

Keeping in mind the small number of data points left with Model ln-1C (and the failed ln-1D & ln-1E): does including fossil data help alleviate this issue enough to create accurate pred-$M_1$Age for *H. erectus* and fossil hominins? Model ln-2E (Hominid, Extant & Extinct) failed to meet basic regressions criteria, presumably again due to the low data set size ($n = 9$). Model ln-2C (Catarrhine, Extant & Extinct) pred-$M_1$Age for *H. erectus* is over-predicted above RC. Model ln-2D (Hominoid, Extant & Extinct) pred-$M_1$Age for *H. erectus* is over-predicted above AC. Compared with ln-2B, the residual for *H. erectus* decreases with ln-2C and decreases again with ln-2D. The overall accuracy of pred-$M_1$Age for the species used to build the models, however, decreases with ln-2C and again with ln-2D. *H*a-$M_1$Ages were not within AC for *H. erectus* using either ln-2C or ln-2D. Progressively excluding the fossil-inclusive data set did not significantly improve the prediction for *H. erectus*.

### Section 7.2.4 Varying the Equation Type

This section now discusses the models which used different equation types, employing the methods mentioned above. First the extant only data set models are presented, followed by the fossil-inclusive data set models.

#### Section 7.2.4.A Set 1 Models

With both the Linear and the Polynomial equations, Group 1D (Hominoid) and Group E (Hominid) do not pass initial criteria, again likely due to the small data set sizes ($n < 10$). The discussion will start with the polynomial equation models, followed by the linear models.

#### Polynomial Models

Second level (quadratic) and third level (cubic) polynomial equation models were repeated for all of the previous steps. The cubic equations performed better than the quadratic equations with the Set 1 data, and are favoured for discussion of Set 1. In all of the Cubic models, extant *H. sapiens* is predicted so accurately that the *H*-residuals cannot be applied as adjustments.

Cubic-1A (Primate, Extant Only) pred-$M_1$Age for *H. erectus* is within RC, but not AC. No other fossil hominin is predicted within AC, and only *H. neanderthalensis* is within RC. Cubic-1B (Haplorhine, Extant Only) is within lower limit of AC, and Cubic-1C is within upper limit of AC. However, in both of these models, only *H. neanderthalensis* is within AC, other fossil hominin pred-$M_1$Ages are over-predicted above RC. In the majority of the Cubic and Quadratic Set 1 models, pred-$M_1$Age is accurate in only 55% (or less) of the species used to build the models. Cubic-1A is accurate for 67%, however the majority of the pred-$M_1$Ages for the hominoid species are not accurate.

### Linear Models

Linear-1A (Primate, Extant Only) and Linear-1B (Haplorhine, Extant Only) pred-$M_1$Age for *H. erectus* is above RC. With both models, pred-$M_1$Age is within AC for Australopiths, but above RC for the other fossil hominins. Linear-1C (Catarrhine, Extant Only) pred-$M_1$Age for *H. erectus* is within RC, within AC for Australopiths and *H. neanderthalensis*, but above RC for Fossil *H. sapiens*. *H*-residual and *P*-residual adjustment does not bring the fossil hominins uniformly within AC overall. In the Linear Set 1 models, pred-$M_1$Ages are only accurate in 46% (or less) of the species used to build the models. In short none of the Linear or Cubic Set 1 models produce accurate $M_1$Age predictions across the fossil hominins as a group, nor within *Homo* species as a group.

## Section 7.2.4.B Set 2

In the Set 2 Models, the Quad models performed better than the Cubic models, so the Quad models are addressed here. This section will cover the polynomial (quadratic) models first and then the linear models.

### Polynomial

Pred-$M_1$Age for *H. erectus* is outside of RC in all the Set 2 Quad models. Some are within RC for other fossil hominins, but only Quad-2A is within AC, but not uniformly within AC for all of them. Adjustment with *H*-residuals and *P*-residuals did not result in values within AC uniformly across the fossil hominins.

For the Cubic and Quad Set 2 models, pred-$M_1$Age is only accurate in 56% (or less) of the species used to build the models.

### Linear

Pre-$M_1$Age for *H. erectus* is outside of RC in Linear-2A (Primate,Extant & Extinct), and within RC but outside of AC in the rest of the Linear Set 2 models. Applying *H*-residuals and *P*-residuals resulted in some fossil hominins being within AC in some of the Linear Set 2 models, but no model brings all fossil hominins within AC uniformly. Linear-2C (Catarrhine, Extant & Extinct) *H*a-$M_1$Age is within at least RC for all 4 fossil hominin test points, but the *H*a-$M_1$Age for the Australopiths is less accurate then it’s non-adjusted pred-$M_1$Age. Linear-2D *H*a-$M_1$Age and Linear-2E *H*a-$M_1$Age are within at least RC across. However Linear-2D is only within AC with 2 of the 4, and Linear-2E (Hominid, Extant & Extinct) is only within AC with the Australopiths. The Linear Set 2 models are only accurate for 47% (or less) of the species used to build the models.

## Section 7.2.5 Summary

Looking back across all 40 models created, no model creates accurate predictions of $M_1$Age across all 4 fossil hominins. While it is possible that none of the $M_1$Age estimates being used for these test points is accurate. It is also possible that fossil *H. sapiens* did not yet have the same $M_1$Age as modern *H. sapiens*. If we accept, for this exercise, that Late Pleistocene Fossil *H. sapiens* are likely to have the $M_1$Age used for the AC, then 3 of the 4 fossil hominin $M_1$Age points were also used in the construction the Set 2 models and 1 of the 4 was used in the construction of the Set 1 models.

The models (and past models) have either high or very high positive correlation, and with this high correlation between ECV and $M_1$Age, the correlation might be expected to produce accurate predictions. However, $M_1$Age/ ECV regressions produce such wide 95% prediction intervals that another study found that Australopith $M_1$Age could be predicted from well below hominid $M_1$Ages to within $M_1$Age ranges for *H. sapiens* (Kelley & Schwartz 2012). Even with variation in data set sizes, and differences in data points used for extant hominids, this lack of precision they noted is similar in the lack of precision in the 40 models generated in this study.

## Section 7.3 Issues when Applying Models

As demonstrated in the results, choice of fitting method impacts the prediction results. Simply by employing bivariate regression, the presumption that the variable y ($M_1$Age ) is dependent on the variable x (ECV) has been made. The impact of phylogenetic inertia on $M_1$Age variation could not necessarily be corrected for without reducing the size of the data sets, potentially making them too small for the methods being employed here. There may be other regression methods not explored here could overcome this.

Another issue that should be noted in the application of regressions for prediction of $M_1$Age, is that the composition of the population that the regression is applied to impacts the results in ways that could be conflated with actual between-group variation in life history schedules. In Chapter 6, the figures demonstrated how, across the models, the ranges of predictions that individual fossil hominin ECVs produced could be very wide. If *H. e. erectus* is separated into regional groups, the average ECV for each region can look very different: African = 855 ml; Southeast Asian = 946 ml; East Asian = 1029 ml. Using Model ln-1A (Primate, Extant Only) as an example here, this results in a spread of 1 year between the average pred-$M_1$Ages of the African and East Asian groups. This is an artefact of linear regression which has the potential to be interpreted as real biological differences in molar emergence timing between these populations.

Within fossil species, any group represented by a small population, has the potential to later be described as part a larger group, and may not metrically represent mean ECV of said larger group. Treating potential sub-specifics as separate species could also generate misleading predictions. For instance, *H. e. ergaster* group ECV = 801 ml, African *H. e. erectus* group ECV = 855 ml but an African *H. erectus/ergaster* group ECV = 839 ml. Treating them separately creates the appearance of metric variation in pred-$M_1$Age, where there complete overlap of *H. ergaster* pred-$M_1$Ages by African *H. e. erectus*.

Conversely, grouping two potentially separate species into a single specific can artificially inflate or reduce the combined mean where the combined groups don't fully overlap metrically. For instance upper range of ECV for Southeast Asian *H. erectus* would appear to be greater than than the African and East Asian *H. erectus* if the *H. soloensis* population is not treated as a separate species. Separately, Southeast Asian *H. erectus* = 922 ml and *H. soloensis* = 1140 ml, while including *H. soloensis* in Southeast Asian *H. erectus* ECV = 1023 ml. These differences in means produce different predicted $M_1$Age, which can not necessarily be interpreted as different life history schedules between these fossil specimen populations.

*H. neanderthalensis* and *H. sapiens* (fossil and extant) demonstrate a large degree of overlap for ECV (ml). As noted in Chapter 4, the published $M_1$Age estimate for *H. neanderthalensis* = 6.7 yr (Macchiarelli *et al.* 2006). With $M_1$Age which is greater than *H. sapiens*, but a slightly lower average ECV, *H. neanderthalensis* is an instance of where regression predictions cannot accurately predict variation between closely related species/sub-species when the independent variable is similar. Fossil *H. sapiens* have a larger ECV than both modern *H. sapiens*. This ECV value is similar to (but slightly larger than) *H. neanderthalensis,* leading to fairly similar $M_1$Age prediction values: which will mean that in a given model there is either and over-prediction for fossil *H. sapiens* or and under-prediction for *H. neanderthalensis*.

The *H. erectus* s.l. hypodigm varies significantly for ECV: there is a range from lowest to highest coming in at just over 500 ml when including *H. e. ergaster*; the range is over 600 ml if the *H. e. georgicus* population is also included; and as much as 700 ml if the *H. soloensis* fossils are included. *H. erectus/ergaster* also overlaps significantly with other species. ECV for *extant* AMH can be as low as 900 ml for some outlier populations, for instance. Without an understanding of how ECV and $M_1$Age vary together at population or individual levels in extant humans (or how they covary with other relevant variables) it is difficult to have a good framework for how variations in pred-$M_1$Ages between fossil hominin species are interpreted.

When interpreting predicted or estimated $M_1$Age of fossil hominins, there is a tendency to refer to species with ages which are closer to non-human hominid $M_1$Age as “Ape-like” or “Human-Like”. Additionally, this doesn’t address the complexity of interpreting pred-$M_1$Age results for AMH. The line of regression for Haplorhine species says that *H. sapiens* $M_1$Age should be > 7 yr (Smith *et al.* 1995; Kelley & Schwartz 2012), yet *H. sapiens* $M_1$Age is about 5.9 yr. This has been interpreted to indicate that *H. sapiens* have “dissociated” from the correlation of $M_1$Age and ECV (Kelley & Schwartz 2012). However, depending on how one defines mean ECV for AMH, pred-$M_1$Age can vary within a model. In Model ln-1B (Haplorhine, Extant Only), 1295 ml returns 7.0 yr and 1350 ml returns 7.2 yr. However, when using a different regression type the prediction is lower. With Linear-1B, 1295 ml returns just 6.6 yr. With Cubic-1B, 1295 ml returns just 5.5 yr. Whether *H. sapiens* $M_1$Age/ECV is "dissociated" from the expected depends on the equation type used, the species used in building the model, and how *H. sapiens* mean ECV is defined.

If the regression line in itself is treated as an accurate reflection of life history differences (e.g. biological grades), then a hypotheses which explains why humans $M_1$Age has *not* extended as greatly as would be predicted by the regression is needed. When a fossil hominin pred-$M_1$Age that is greater than observed $M_1$Age of Australopiths, but smaller observed age for humans, should this be interpreted as the species displaying mild divergence from the ancestral state (relative to humans) or should this be interpreted as the species having a similarly divorced $M_1$Age correlation, like AMH? If, however, the dissociation in AMH is treated as an artefact of bivariate regression, then inferring a dissociation for either AMH or fossil hominins would be an inappropriate application of pred-$M_1$Age. When ascribing an "ape-like", "intermediate", or even "unique" pattern of LH to fossil hominins based on $M_1$Age values which are below the human range, the assumption is that an absolute $M_1$Age value difference represents a significantly different total variation LH schedule pattern, and that any fossil hominin $M_1$Age below that of humans is due to LH pattern inertia, rather than to either prediction error or a variation between the selective regimes shaping the life history schedules of humans and other hominins. In other words, it cannot be assumed that *H. erectus* has a "intermediate" $M_1$Age value because the LH pattern of humans had not yet "fully" evolved. This presumes a linear "trajectory" of hominid evolution towards the "extended" human life history schedule. Assigning "intermediate" or "ape-like" positions to fossil hominins also requires that we treat the *P. troglodytes* $M_1$Age as representative of the non-human hominids. $M_1$Age continues to be under-documented across extant hominids, and *P. troglodytes* continues to be our best documented species. However, despite low degree of ECV variation amongst extant non-human hominids (ranging ~ 150 ml between the species included in the models compared to a range of up to ~1000 ml across fossil hominins), the available evidence suggests considerable $M_1$Age and life history schedule variation amongst the extant hominids (e.g. Benyon *et al.* 1991; Mikeliban *et al.* 2021; Wich *et al.* 2004; Winkler *et al.* 1996). Applying the same standards of comparison, *P. pygmaeus* could be said to have an "intermediate" $M_1$Age/LH pattern. If *P. pygmaeus* (4.6 yr) were made the "ape-like" standard, then *H. erectus* is no longer intermediate between extant hominids and AMH.

It is also important to remember, that with this primate data, the regression is potentially violating the required assumptions of a causal link between the y-value (dependent) and the x-value (independent). There is no direct evidence that increase in ECV causes increase in $M_1$Age: as the y-value, $M_1$Age is assumed to be the dependent value. The data is also not normally distributed, and the number of points is undesirably small.

The sub-fossil Strepsirrhines offer examples where larger ECV size is not directly related to $M_1$Age similarly to closely related extant Strepsirrhines. There is variation above and below the expected $M_1$Age pattern for $M_1$Age at similar ECV. The *H. neanderthalensis* $M_1$Age estimate of 6.7 yr, is later than AMH $M_1$Age. This complicates interpretations for fossil hominins with pred-$M_1$Ages intermediate between AMH and extant hominids, as it evidences the possibility of fossil hominin $M_1$Age falling outside of linear trajectory from "ape-like" to "human-like". The impact that group size and environmental differences appear to have on the life history variables (e.g. IBI, weaning, etc) and molar emergence timing of the similarly ECV-sized *Pan* (3.2—3.8 yr) and *Pongo* (4.6 yr) are further factors which complicate the use of pred-$M_1$Age for fossil hominin $M_1$Age estimates, and the interpretation of differences between pred-$M_1$Age and estimated or observed $M_1$Age in hominins.

Does life history regression actually provide a reasonably accurate picture of the life history patterns of fossil hominins? Bivariate regression has the potential to specify $M_1$Age variation between two groups which vary metrically for ECV but which are grouped based on non-metric morphology. It also has the potential to be *unable* to identify existing $M_1$Age variation in two populations which are morphologically differentiated but which have similar/overlapping ECV ranges (e.g. *H. sapiens* and *H. neanderthalensis*). It also has the potential for skewed predictions if a fossil population ECV is based on a (necessarily) small sample size of fossils. Small samples have the potential to actually represent outlier values within a larger fossil population whose range is, as yet, not fully identified. The history of the *H. erectus* hypodigm itself provides excellent examples of a fossil species with regularly changing parameters as additional fossil discoveries increase the information available for the species. New fossils have also increased the information available for making cross-species comparisons with *H. erectus*. I employed alternate designations of populations which could also be considered as part of the *H. erectus* hypodigm (e.g. *H. e. ergaster,* or *H. soloensis*) in order to highlight where a metric overlap of these populations could result variation in predicted $M_1$Age, which could be  potentially be interpreted as LH schedule variation. If a subgroup later is found to not accurately represent the larger group that it later is ascribed to, LH schedule and LH evolutionary assumptions may be found to have been prematurely assigned. Separating fossil populations into species or sub-species based on traits or assumptions which may not *necessarily* represent a *speciation event* has the potential to lead to the appearance of variation based on the taxonomic assignment. Further applying these assumed predicted variations to the description of the two populations can lead to reinforcement of the assumption of speciation-events between the two populations.

Where newly described fossil samples are deemed to warrant assignment of a novel specific or taxon, subsequent additions to the hypodigm might lead to the expansion of the range of that species, meaning the once seemingly very clear differences between it and other species become less clear. Where a population A was originally differentiated from population B, and the two are later synonymised, the ranges of both previously separated populations is expanded into a new unified range, which may impact past contrasts between A or B and another species/population (e.g. A is was seen as much smaller than C, and B was intermediate to both, the mean or range of AB may not be as significant as between A and C). Caution should taken when applying predictions to species means derived from a fossil population with a relatively small samples size. Further, extrapolations from said predictions, such as inferring phylogeny or life history patterns, are not necessarily appropriate.

Overall, many researchers have encountered issues with estimating $M_1$Age from ECV. Robson & Wood (2008) found that body mass to be a better predictor of life history events in hominids, and urge caution in making life history inferences from dental eruption timing. Kelley & Schwartz (2012) have identified the substantially large prediction interval ranges of $M_1$Age/ECV regressions. Bermúdez de Castro *et al.* (2015) have urged caution in drawing conclusions from dental development data in general—and $M_1$Age data more specifically—about the prolongation of life stages in earlier hominins, especially at the species level. Smith (2013) urges caution in using M1 eruption timing to predict weaning age (and by extension other LHVs, such as IBI), as the age of weaning does not equal $M_1$Age in *P. troglodytes*, as had previously been assumed. The results of this study agree with these findings, with regard to the inability of pred-$M_1$Age to accurately estimate across the available fossil hominin $M_1$Age (histology-calculated) estimates.

As a further example it the recently described *Homo naledi* fossils, which are thought to represent a late-surviving (~0.3 Mya) mosaic *Homo* species. The *H. naledi* hypodigm is relatively small in cranial size (ECV = 513 ml) for it's late geological age (Berger *et al.* 2015; Dirks *et al.* 2017).

In an analysis of mandibles from two *H. naledi* juveniles, the species is described as being similar to AMH in the *sequence* of permanent tooth emergence (Cofran & Walker 2017).[38] Because the ECV of the two species differs by over 800 ml, my $M_1$Age/ECV regressions would not predict *H. naledi*'s permanent molar timing to be as similar to *H. sapiens* permanent molar emergence timing as the Cofran & Walker (2017) tooth sequence study found it's dental *sequence* to be relative to *H. sapiens* sequence.

The wide range of predictions returned when applied to individual observed ECVs indicates that caution is urged when applying these regressions below the level of temporally grouped *Homo* species (however note the issues potentially presented by *H. naledi,* late ). Fossil *Homo* species cranial and post-cranial skeletal elements can vary widely even within individuals recovered from a single

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[38] At the same time, however, *H. naledi* appears to have a more "primitive" sequence of *deciduous* tooth emergence (Cofran & Walker 2017).

locality. Metric variation can be sexually dimorphic, the degree of which may not be fully understood within fossil *Homo* species, especially when insufficient samples are yet available for that population. Caution is warranted when implying life history pattern or life history traits based on pred-$M_1$Age calculated for species from which the ECV mean is derived from a very limited sample size.

Longitudinal studies and larger sample sizes are needed across most primate species for life history and life history related variables (Bermúdez de Castro *et al.* 2015). The quality of the primate reference sample also needs to be systematically improved. Even when simply assessing levels of size variation and sexual dimorphism in *extant* primates, osteological collections of museums cannot be used to accurately test hypotheses about comparative differences in controlled contexts because they were not collected systematically (Plavcan 2012). Recent studies designed to measure adrenarche/gonadarche to allow for interspecies comparison using non-invasive collection of specimens to test hormonal markers are a promising start (Berghänel *et al.* 2023). Smith (2013) suggests future studies which obtain direct weaning ages through fine-scaled tooth chemistry.

Future studies which increase the number of histologically derived $M_1$Ages for fossil hominins would serve to improve the understanding of fossil hominin $M_1$Age variation. $M_1$Age estimates from molars in association with crania (e.g. where $M_1$Age and ECV can be paired for a distinct population). It is understandable that more complete fossils have been less available for analysis because of the concerns for damage (e.g. ground sections), newer synchrotron microscopy methods (Tafforeau & Smith 2008; Smith *et al.* 2015) show promise for obtaining more histologies. There is still the inescapable limit of the number of available fossils at or near M1 emergence. Nonetheless, a larger sample of histological $M_1$Ages is needed to better describe the variation of $M_1$Age in fossil hominins.

# Chapter 8

# Chapter 8 Conclusions

Because the pattern of human life history appears to be very different from that of other primates, paleoanthropology is understandably interested in estimating and understanding the life histories of fossil hominins in order to understand how our life history pattern evolved. Regressions of extant primate variables--using the available species data to form a comparative reference set for fossil hominin life history--have been used as predictive equations to estimate fossil hominin life history variables and, by extension, their life history patterns..

Within the context of understanding the human evolutionary lineage, *H. erectus* s.l. has historically been an important species because it was (as *Pithecanthropus*) the first known pre-Neanderthal fossil hominin species. For a considerable amount of time *H. erectus* was considered the first species within the genus *Homo* to have a human-like body plan suited for bipedalism. They were an important species to estimate early *Homo* life history evolution for.

Because molar emergence appears to be correlated to other key life history variables, and is highly correlated to ECV, regressions of $M_1$Age to ECV were used to estimate fossil hominin species' $M_1$Age, including *H. erectus,* in the mid-1990s. There has subsequently been an increase (and change of species definitions) in the fossil hypodigm of *H. erectus* s.l. There has also been a histological $M_1$Age published for *H. erectus*, in 2001. It was assumed that the publish primate reference sample for $M_1$Age would have increased in that time, and that this could be employed alongside the histological age for *H. erectus* to test the accuracy of regression predictions applied to fossil *Homo* species..

This study found that the extant primate data reference data set could be moderately increased, however issues persist in primate life history variables: uneven sampling effort; small numbers of species represented in the available data; the small sample sizes used to calculate many of the available species' means. This study, novelly, added histologically derived $M_1$Ages for extant and extinct species to the reference sample, to generate comparative models to be tested.

In exploring whether the previously published regression methodology, when repeated with expanded extant primate reference data sets alone, the pre-existing methodology predicted $M_1$Age for *H. erectus* over the test range upper limit. With no additional changes in methodology, the model created adding fossil species data points did not improve the accuracy of predictions.

Changing the taxonomic exclusion criteria, one model using the original regression type passed the initial stage test range: ln-2D (Hominoid only group, including fossil species data points). Using only extant primate data points (Set 1), the Cubic- and Linear- models when modelled using Group 1B (Haplorhine, Extant Only)[39] met the RC. When, Cubic- and Linear- applied to data set created by increasing taxonomic exclusion by one step, (Group 1C: Catarrhine-only, extant data points) the predictions also met the primary inclusion criteria. Using

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[39] e.g. the model group based on the historically applied taxonomic level restrictions

the Set 2 groups, Quadratic-2D and 2E, as well as linear 2-C and 2D produced predictions that passed primary stage test range criteria.

In the second stage of analysis, applied to an extended range of fossil Hominin ECVs, all models produced results suggesting issues with accuracy the lowest taxonomic levels (e.g. species), urge caution in generating predictions for new fossil hominin $M_1$Ages. Based on the existing primate and fossil reference data set, regression models appear to lack the sensitivity to identify $M_1$Age variation between fossil hominin species/groups which are morphologically differentiated but which overlap metrically for ECV. Due to a high level of sensitivity of the predictions to variations in ECV: where new species have the potential to represent outlier values within a larger mean. The results demonstrate that there is potential for outlier-groups to skew $M_1$Age predictions when treated as a species-grou*p.* Furthermore, recent studies have demonstrated that the link between certain life history variables in hominids—such as weaning age and interbirth intervals—are not as directly tied to $M_1$Age as had been previously thought. Other researchers have urged caution when applying "human-like" or "chimpanzee-like" dental development models to fossil hominin species which are intermediate in timing and potentially demonstrating a mosaic of traits with regards to their pattern of dental development.

Applying *H*-residuals or *P*-residuals does not improve the fit or pred-$M_1$Age uniformly across fossil hominins. Caution is urged with this sort of ad hoc adjustment, because co-variation in fit is not uniform and variation from the line of regression changes with each model. This variation is more likely to be an artefact of the model, rather than a representation of biology.

Taken as a whole, this study concludes that despite the correlation between these two variables, pred-$M_1$Age in $M_1$Age/ECV primate regression models is not accurate to fossil hominins $M_1$Age estimates or to the data points used to create the models. Caution is be urged against estimating life history patterns from pred-$M_1$Age for fossil *Homo* species, at species/sub-species level, and against projecting life history patterns onto fossil hominin species based on said pred-$M_1$Age.

Issues identified with sampling effort errors within the reference data highlights the need for systemised studies to collect more comprehensive and reliable extant primate life history data in general and larger data sets for $M_1$Age more specifically (with a focus on healthy, in-vivo sample populations). Also emphasised is the need for studies which increase the number of fossil hominin $M_1$Age estimates (e.g. through histological methods), in order to understand how this variable is expressed across the wide temporal and geographic spread of *H. erectus* s.l. populations and comparative fossil *Homo* species more generally. However, even with a more detailed and extensive primate data set, it is likely that bivariate regression will not be the correct tool for estimating fossil hominin $M_1$Age. The ultimate picture of the evolution of the unique human life history pattern has the potential to be both more and less complex than we have assumed. Due to the nature of bivariate regressions, $M_1$Age/ECV models are likely to remain an inaccurate method for estimating fossil hominin $M_1$Age, with undesirably large prediction intervals.

# Appendices

# Appendix 1. Primate Data

## Appendix 1.a. Primate Data: $M_1$Age

| Species | $M_1$Age (years) | n = | Reference |
|---|---|---|---|
| *Cheirogaleus medius* | 0.1 | 2 | (Smith *et al.* 1994) |
| *Avahi laniger* | 0.1 | 2 | (Godfrey *et al.* 2003) |
| *Propithecus verreauxi* | 0.2 | 1 | (Smith *et al.* 1994) |
| *Eulemur fulvus* | 0.4 | 2 | (Smith *et al.* 1994) |
| *Eulemur macaco* | 0.4 | 2 | (Smith *et al.* 1994) |
| *Lemur catta* | 0.3 | 2 | (Smith *et al.* 1994) |
| *Varecia variegata* | 0.5 | 2 | (Smith *et al.* 1994) |
| *Galago senegalensis* | 0.1 | 1 | (Smith *et al.* 1994) |
| *Lepilemur leucopus* | 0.1 | 1 | (Godfrey *et al.* 2003) |
| *Callithrix jacchus* | 0.3 | 120 | (Smith *et al.* 1994) |
| *Saguinus fuscicollis* | 0.4 | 62 | (Smith *et al.* 1994) |
| *S. nigricollis* | 0.3 | 14 | (Smith *et al.* 1994) |
| *Aotus trivirgatus* | 0.4 | 38 | (Smith *et al.* 1994) |
| *Cebus albifrons* | 1.1 | 17 | (Smith *et al.* 1994) |
| *C. apella* | 1.2 | 6 | (Smith *et al.* 1994) |
| *Saimiri sciureus* | 0.4 | 11 | (Smith *et al.* 1994) |
| *Chl. aethiops* | 0.8 | β | (Smith *et al.* 1994) |
| *Macaca fascicularis* | 1.4 | β | (Smith *et al.* 1994) |
| *M. fuscata* | 1.5 | 270 | (Smith *et al.* 1994) |
| *M. mulatta* | 1.4 | 72 | (Smith *et al.* 1994) |
| *M. nemestrina* | 1.4 | 72 | (Smith *et al.* 1994) |
| *Mandrillus sphinx* | 2.1 | 88 | (Setchell & Wickings 2004) |
| *Papio anubis* | 1.7 | 57 | (Smith *et al.* 1994) |
| *P. cynocephalus* | 1.7 | >20 | (Smith *et al.* 1994) |
| *P. hamadryas* | 1.6 | 1 | (Dirks & Bowman 2007) |
| *S. entellus priam* | 1.5 | 1 | (Dirks & Bowman 2007) |
| *Hylobates agilis* | 1.4 | 2 | (Uchikoshi & Matsuzawa 2007) |
| *H. lar* | 1.8 | 3 | (Dirks & Bowman 2007) |
| *S. syndactylus* | 2.3 | 3 | (Dirks & Bowman 2007) |
| *Gorilla gorilla* | 3.5 | $2^{\alpha}$ | (Schwartz *et al.* 2006; Kelley & Schwartz 2010) |
| *Homo sapiens* | $5.9^{\delta}$ | ε | (Liversidge 2001, 2003) |
| *Pan troglodytes** | 3.2 | 38 | (Kuykendall *et al.* 1992) |
| *Pongo pygmaeus* | 4.6 | 1 | (Kelley & Schwartz 2010) |

**Table 9.1 Primate $M_1$Age (years)**

* - Unsure of sub-species used; α - based on 2 individuals which correspond with a previous n=? personal as noted in Smith, et al. (1995); β - "unstated", but appears to be calculated from n>1 individuals; δ - three ages are listed: alveolar, midpoint, and occlusal; ε - unable to ascertain due to study composition, cross-population/historical-era study

## Appendix 1.b. Primate Data: ECV (ml)

| Species | ECV (ml) | n = | Source |
|---|---|---|---|
| *Cheirogaleus medius* | 3 | 7 | (Isler *et al.* 2008) |
| *Avahi laniger* | 10 | 13 | (Isler *et al.* 2008) |
| *Propithecus verreauxi* | 26 | 7 | (Isler *et al.* 2008) |
| *Eulemur fulvus* | 26 | 8 | (Isler *et al.* 2008) |
| *Eulemur macaco* | 25 | 8 | (Isler *et al.* 2008) |
| *Lemur catta*‡ | 22 | 10 | (Isler *et al.* 2008) |
| *Varecia variegata* | 32 | 8 | (Isler *et al.* 2008) |
| *Galago senegalensis* | 4 | 192 | (Isler *et al.* 2008) |
| *Lepilemur leucopus* | 7 | 9 | (Isler *et al.* 2008) |
| *Callithrix jacchus* | 7 | 7 | (Isler *et al.* 2008) |
| *Saguinus fuscicollis*† | 8 | 22 | (Isler *et al.* 2008) |
| *Saguinus nigricollis* | 9 | ? | (Smith *et al.* 1995) |
| *Aotus trivirgatus* | 17 | 12 | (Isler *et al.* 2008) |
| *Cebus albifrons* | 65 | 30 | (Isler *et al.* 2008) |
| *Cebus apella*† | 67 | 48 | (Isler *et al.* 2008) |
| *Saimiri sciureus*† | 24 | 86 | (Isler *et al.* 2008) |
| *Chlorocebus aethiops* | 65 | 53 | (Isler *et al.* 2008) |
| *Macaca fascicularis*† | 64 | 97 | (Isler *et al.* 2008) |
| *Macaca fuscata* | 103 | 22 | (Isler *et al.* 2008) |
| *Macaca mulatta*† | 86 | 21 | (Isler *et al.* 2008) |
| *Macaca nemestrina* | 106 | 21 | (Isler *et al.* 2008) |
| *Mandrillus sphinx* | 152 | 19 | (Isler *et al.* 2008) |
| *Papio anubis* | 167 | 30 | (Isler *et al.* 2008) |
| *Papio cynocephalus* | 163 | 25 | (Isler *et al.* 2008) |
| *Papio hamadryas* | 150 | 14‡ | (Isler *et al.* 2008) |
| *S. entellus priam* | 83 | 12 | (Isler *et al.* 2008) |
| *Hylobates agilis* | 102 | 177 | (Isler *et al.* 2008) |
| *Hylobates lar*† | 91 | 16 | (Isler *et al.* 2008) |
| *S. syndactylus* | 122 | 35 | (Isler *et al.* 2008) |
| *Gorilla gorilla* | 490 | 54 | (Isler *et al.* 2008) |
| *Homo sapiens* | 1350 | — | (Beals *et al.* 1984) |
| *Pan troglodytes*† | 365 | 102 | (Isler *et al.* 2008) |
| *Pongo pygmaeus*† | 377 | 80 | (Isler *et al.* 2008) |

**Table 9.2 Primate ECV (ml)**
caption here
† Groups subspecies together
‡ Wild and captive combined

## Appendix 2. SubFossil Lemur Data

| | ECV* (ML) | $M_1$AGE (YEARS) | $M_1$AGE REFERENCES |
|---|---|---|---|
| *Archaeolemur majori* | 93 | 1.3 | Godfrey *et al.* (2006) |
| *Hadropithecus stenognathus* | 106 | 2.8 | Catlett *et al.* (2010) |
| *Megaladapis edwardsi* | 136 | 0.9 | Schwartz *et al.* (2007) |
| *Mesopropithecus globiceps* | 41 | 0.6 | Catlett *et al.* (2010) |
| *Palaeopropithecus ingens* | 80 | 0.2 | Godfrey *et al.* (2006) |

**TABLE 9.3 SUBFOSSIL LEMUR ECV & $M_1$AGE**
*All ECVs references are Catlett *et al.* (2010)

## Appendix 3. Miocene Ape Data

### Appendix 3.a. Miocene Ape Data: $M_1$Age

| | $M_1$AGE (YEARS) | SOURCE |
|---|---|---|
| *Afropithecus turkanensis* | 3.0 | Kelley (1997) |
| *Hispanopithecus hungaricus* | — | — |
| *Hispanopithecus laietanus* | 3.6 | (Dean & Kelley 2011)) |
| *Proconsul heseloni* | 3.4 | Benyon *et al.* (1998) |
| *Sivapithecus parvada* | 3.4 | Kelley (1997); Kelley & Smith (2003) |

**TABLE 9.4 MIOCENE APE $M_1$AGE (YEARS)**

### Appendix 3.b. Miocene Ape Data: ECV

| | ECV (ml) | Source |
|---|---|---|
| *Afropithecus turkanensis* | — | — |
| *Hispanopithecus hungaricus* | 329 | Alba (2010) |
| *Hispanopithecus laietanus* | — | — |
| *Proconsul heseloni* | 167 | Alba (2010) |
| *Sivapithecus parvada* | — | — |

**TABLE 9.5 MIOCENE APE ECV (ML)**

# Appendix 4. Fossil Hominin Data

## Appendix 4.a. Fossil Hominin Data: $M_1$Age

| | $M_1$AGE (YEARS) | SOURCE |
|---|---|---|
| *A. afarensis* | 2.9 | Kelley & Schwartz (2012) |
| *A. africanus* | 3.2 | Kelley & Schwartz (2012) |
| *P. boisei* | 3.0 | Kelley & Schwartz (2012) |
| *P. robustus* | 3.1 | Kelley & Schwartz (2012) |
| *H. neanderthalensis* | 6.7 | Macchiarelli *et al.* (2006) |

**TABLE 9.6 FOSSIL HOMININS: KEY SPECIES: $M_1$AGE DATA**

## Appendix 4.b. Fossil Hominin Data: ECV

| | ECV (ML) | SOURCE |
|---|---|---|
| *A. afarensis* | 455 | DeSilva (2011) |
| *A. africanus* | 462 | DeSilva (2011) |
| *P. boisei* | 495 | DeSilva (2011) |
| *P. robustus* | 530 | DeSilva (2011) |
| H. *neanderthalensis* | 1450 | Guerrero (2019) |

**TABLE 9.7 FOSSIL HOMININS: KEY SPECIES: ECV DATA**

## Appendix 4.c. Fossil Hominins: ECV Data

| GROUP | SPECIES | SPECIMEN | ECV (ML) |
|---|---|---|---|
| Australopiths | *A. afarensis* | | *426* |
| | | AL 162-28 | 400 |
| | | AL 288-1 | 387 |
| | | AL 333-45 | 492 |
| | | AL 444-2 | 550 |
| | | Dikika 1-1 | 300 |
| | *A. africanus* | | *461* |
| | | MLD 1 | 510 |
| | | MLD 37/38 | 435 |
| | | Sts 5 | 485 |
| | | Sts 19/58 | 436 |
| | | Sts 60 | 400 |
| | | Sts 71 | 428 |
| | | Sts 505 | 560 |
| | | Taung | 440 |
| | | Type 2 | 457 |
| | *P. boisei* | | *508* |
| | | KGA-10-525 | 545 |
| | | KNM-ER 406 | 500 |
| | | KNM-ER 407 | 510 |
| | | KNM-ER 732 | 500 |
| | | KNM-WT 13750 | 475 |
| | | OH 5 | 520 |
| | *P. robustus* | | *493* |
| | | SK 54 | 500 |
| | | SK 859 | 450 |
| | | SK 1585 | 530 |

**TABLE 9.8 FOSSIL HOMININS: ECV DATA (AUSTRALOPITHS)**

| GROUP | SPECIES | SPECIMEN | ECV (ML) |
|---|---|---|---|
| Early *Homo* | | | |
| | *H. habilis* s.l. | | *654* |
| | | KNM-ER 1590 | 825 |
| | | OH 24 | 590 |
| | | OH 13 | 650 |
| | | OH 7 | 687 |
| | | KNM-ER 1470 | 752 |
| | | KNM-ER 1813 | 509 |
| | | OH 16 | 638 |
| | | KNM-ER 1805 | 582 |
| | | | |
| | *H. e. georgicus* | | *654* |
| | | D2280 | 780 |
| | | D2282/211 | 650 |
| | | D3444/3900 | 641 |
| | | D4500/2600 | 546 |
| | | | |
| | *H. e. ergaster* | | *801* |
| | | KNM-ER 3732 | 750 |
| | | KNM-ER 3733 | 848 |
| | | KNM-ER 3833 | 804 |
| | | | |

**TABLE 9.9 FOSSIL HOMININS: ECV DATA (EARLY *HOMO*)**

| **Group** | **Species** | **Specimen** | **ECV (ml)** |
|---|---|---|---|
| *H. e. erectus group* | | | |
| | African | | *856* |
| | | Bou-VP-2/66 | 995 |
| | | KNM-WT 15000 | 909 |
| | | KNM-ER 42700 | 691 |
| | | KNM-OL 45500 | 800 |
| | | OH 9 | 1067 |
| | | OH 12 | 727 |
| | | UA 31 | 800 |
| | East Asian | | *1029* |
| | | Hexian | 1025 |
| | | Nanjing 1 | 860 |
| | | Yunxian | 1200 |
| | | Zhoukoudian II | 1030 |
| | | Zhoukoudian III | 915 |
| | | Zhoukoudian V | 1140 |
| | | Zhoukoudian VI | 850 |
| | | Zhoukoudian X | 1225 |
| | | Zhoukoudian XI | 1015 |
| | | Zhoukoudian XII | 1030 |
| | Southeast Asian | | *922* |
| | | Sangiran 2 | 813 |
| | | Sangiran 3 | 950 |
| | | Sangiran 4 | 908 |
| | | Sangiran 9 | 845 |
| | | Sangiran 10 | 855 |
| | | Sangiran 12 | 1059 |
| | | Sangiran 17 | 1004 |
| | | Trinil 2 | 940 |

**TABLE 9.10 FOSSIL HOMININS: ECV DATA (*H. E. ERECTUS* GROUP)**

| GROUP | SPECIES | SPECIMEN | ECV (ML) |
|---|---|---|---|
| Middle Pleistocene *Homo* group | | | |
| | *H. soloensis* | | *1140* |
| | | Ngandong 1 | 1172 |
| | | Ngandong 6 | 1251 |
| | | Ngandong 7 | 1013 |
| | | Ngandong 10 | 1135 |
| | | Ngandong 11 | 1231 |
| | | Ngandong 12 | 1090 |
| | | Ngandong 14 | 1090 |
| | *H. heidelbergensis* | | *1245* |
| | | Arago 21 | 1166 |
| | | Aroerira 3 | 1100 |
| | | Biache | 1200 |
| | | Bodo I | 1250 |
| | | Ceprano | 1165 |
| | | Dali 1 | 1120 |
| | | Ehringsdorf | 1450 |
| | | Kabwe 1 | 1325 |
| | | Jinnuishan | 1390 |
| | | Ndutu | 1100 |
| | | Petralona | 1230 |
| | | Reilingen | 1430 |
| | | Saldanha (Elandsfontein) | 1225 |
| | | Steinheim | 1200 |
| | | Swanscombe | 1325 |
| | *H. antecessor* | | *1208* |
| | | SH4 | 1360 |
| | | SH5 | 1125 |
| | | SH6 | 1140 |

**TABLE 9.11 FOSSIL HOMININS: ECV DATA (MIDDLE PLEISTOCENE *HOMO*)**

| Group | Species | Specimen | ECV(ml) |
|---|---|---|---|
| Late Pleistocene *Homo* | | | |
| | *H. neanderthalensis* | | *1442* |
| | | Feldhofer | 1525 |
| | | Gánovce | 1320 |
| | | Gibraltar 1 | 1200 |
| | | Jebel Irhoud 1 | 1305 |
| | | Jebel Irhoud 2 | 1400 |
| | | Krapina 3 (Cranium C) | 1255 |
| | | Krapina 6 (Cranium E) | 1205 |
| | | La Chapelle-aux-Saints 1 | 1625 |
| | | La Ferrassie | 1640 |
| | | Guattari 1 | 1360 |
| | | Shanidar 1 | 1600 |
| | | Shanidar 5 | 1550 |
| | | Skhul 1 | 1450 |
| | | Skhul 4 | 1554 |
| | | Skhul 5 | 1520 |
| | | Skhul 9 | 1590 |
| | | Spy I | 1305 |
| | | Spy II | 1553 |
| | fossil *H. sapiens* | | *1469* |
| | | Abri Pataud | 1380 |
| | | Arene Candide 1 | 1414 |
| | | Arene Candide 5 | 1661 |
| | | Border Cave | 1510 |
| | | Brno I | 1600 |
| | | Brno III | 1304 |
| | | Coobol Creek | 1444 |
| | | Keilor | 1497 |
| | | Kostenki 2 | 1605 |
| | | Liujiang | 1480 |
| | | Minatogawa 1 | 1390 |
| | | Minatogawa 4 | 1090 |
| | | Nazlet Khater 2 | 1420 |
| | | Omo 2 | 1435 |
| | | Qafzeh 6 | 1568 |
| | | Qafzeh 8 | 1531 |
| | | Singa 1 | 1550 |
| | | Wadjack 1 | 1539 |
| | | Wadjack 2 | 1650 |
| | | Willandra Lakes | 1540 |
| | | Yinkou | 1390 |
| | | Zhoukoudian U.C. 1 | 1500 |
| | | Zhoukoudian U.C. 3 | 1290 |

**Table 9.12 Fossil Hominins: ECV Data (Late Pleistocene *Homo*)**

# Appendix 5. ln-transformed Models

## Appendix 5.a. ln-Models: Equations & Summaries

| **Set 1. Extant Only** | |
|---|---|
| 1A. Primate | ln(y)= 0.7602•ln(x) – 3.2347 |
| 1B. Haplorhine | ln(y)= 0.6220•ln(x) – 2.5043 |
| 1C. Catarrhine | ln(y)= 0.5698•ln(x) – 2.2147 |
| 1D. Hominoid | ln(y)= 0.4821•ln(x) – 1.6280 |
| 1E. Hominid | ln(y)= 0.3626•ln(x) – 0.8626 |
| **Set 2. Extant & Extinct** | |
| 2A. Primate | ln(y)= 0.7225•ln(x) – 3.1427 |
| 2B. Haplorhine | ln(y)= 0.5958•ln(x) – 2.3960 |
| 2C. Catarrhine | ln(y)= 0.5236•ln(x) – 1.9812 |
| 2D. Hominoid | ln(y)= 0.4205•ln(x) – 1.3112 |
| 2E. Hominid | ln(y)= 0.5061•ln(x) – 1.8823 |

**Table 9.13** ln-**transformed Models: Equations**

| | **Set 1 (Extant Only)** | | | **Set 2 (Extant & Extinct)** | | |
|---|---|---|---|---|---|---|
| | **R** | **P** | **Se** | **R** | **P** | **Se** |
| A. Primate | 0.96 | <0.001 | 0.349 | 0.92 | <0.001 | 0.459 |
| B. Haplorhine | 0.97 | <0.001 | 0.210 | 0.96 | <0.001 | 0.229 |
| C. Catarrhine | 0.93 | <0.001 | 0.194 | 0.92 | <0.001 | 0.215 |
| D. Hominoid | 0.94 | =0.002 | 0.188 | 0.87 | <0.001 | 0.217 |
| E. Hominid | 0.79 | =0.212 | 0.213 | 0.82 | =0.007 | 0.193 |

**Table 9.14** ln- **transformed Models: Summaries**

## Appendix 5.b. ln-transformed Models: Predictions

| **ln-transformed Models: Predicted $M_1$Age (years)** | | | | | | | |
|---|---|---|---|---|---|---|---|
| | **1A** | **1B** | **1C** | **2A** | **2B** | **2C** | **2D** |
| *H. erectus* | 7.1 | 5.8 | 5.4 | 6.1 | 5.4 | 5.0 | 4.8 |
| *H. sapiens* | 9.4 | 7.2 | 6.6 | 7.9 | 6.7 | 6.0 | 5.6 |
| *P. troglodytes* | 3.2 | 3.2 | 3.2 | 3.1 | 3.1 | 3.0 | 3.2 |
| Fossil *H. Sapiens* | 10.2 | 7.7 | 7.0 | 8.5 | 7.1 | 6.3 | 5.8 |
| *H. neanderthalensis* | 10.0 | 7.6 | 6.9 | 8.3 | 7.0 | 6.2 | 5.8 |
| Australopiths | 4.3 | 3.8 | 3.7 | 3.8 | 3.6 | 3.5 | 3.6 |

**Table 9.15** ln-**transformed Models**

Comparison table of ln-transformed models: predicted $M_1$Age (years). Because the stage one criteria is not met, ln-1D, ln-1E, and ln-2E were not used for predictions.

## **Appendix 5.c.** ln-**transformed Models: Regressions**

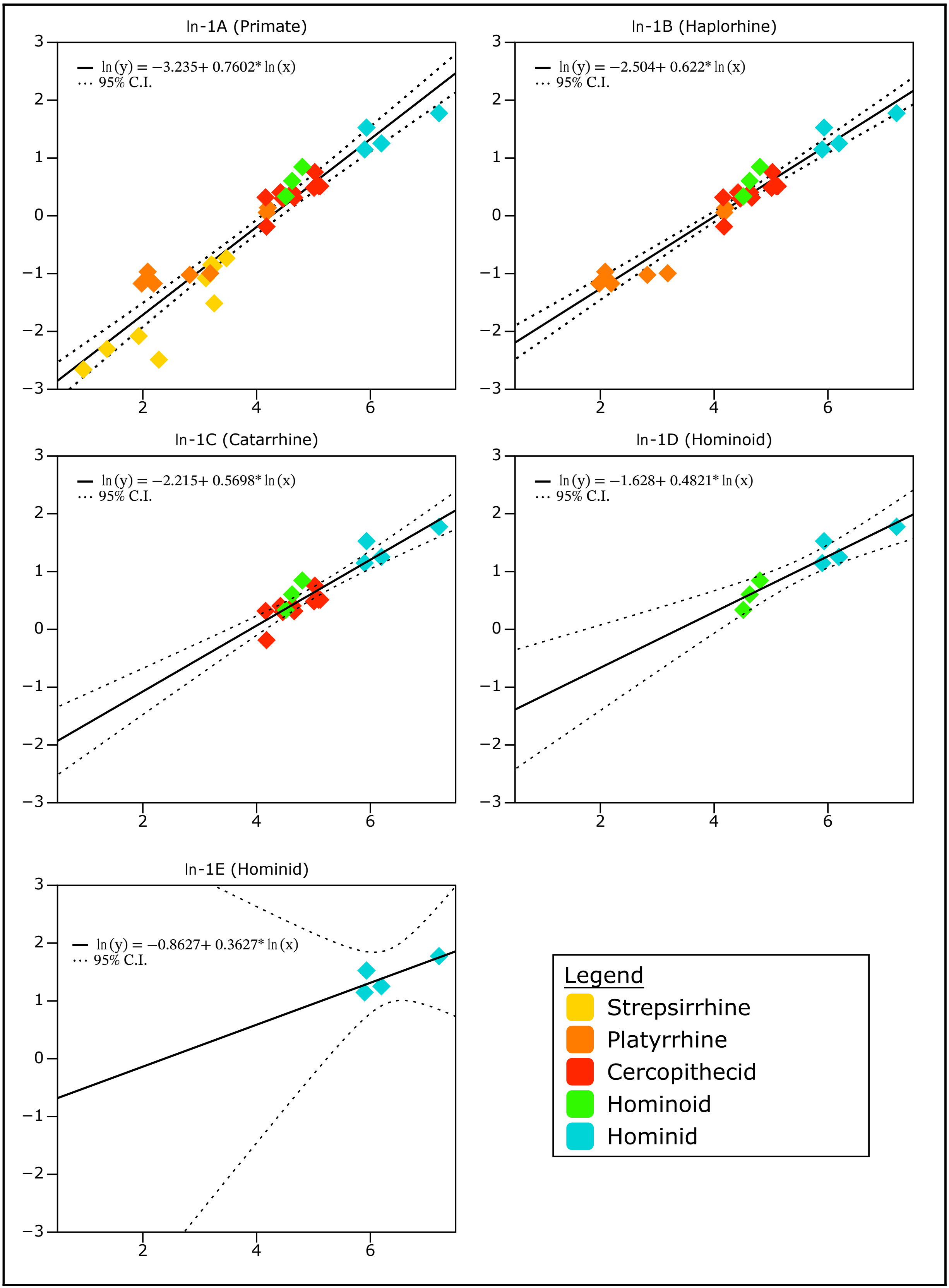

**FIGURE 9.1. REGRESSION PLOTS: ln-MODELS, SET 1**
Comparison of Set 1 (Extant Only) ln-transformed Model box plots of Fossil Hominin predicted $M_1$Age (years).

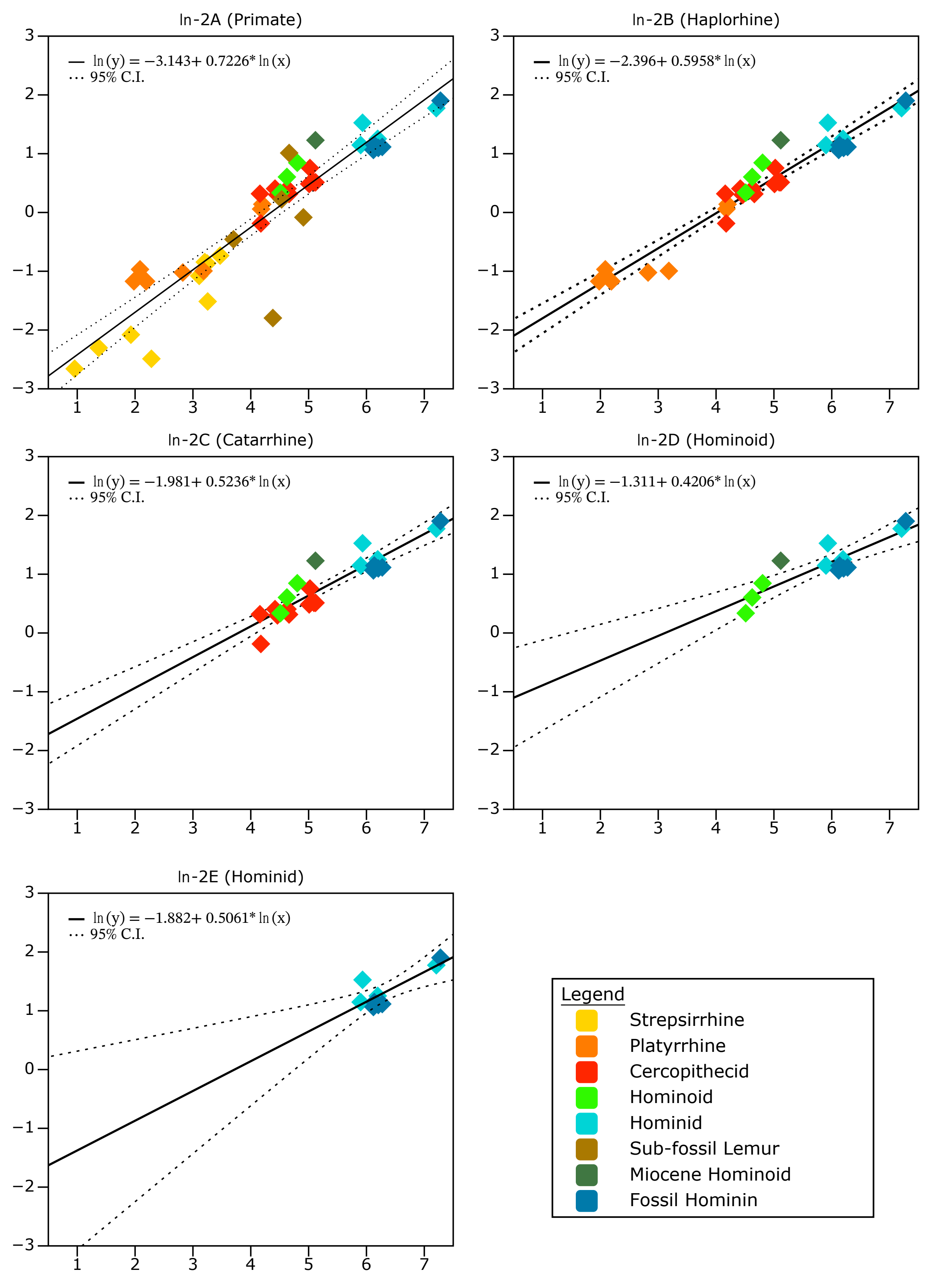

**FIGURE 9.2.** **REGRESSION PLOTS: ln-MODELS, SET 2**

Comparison of Set 2 (Extant & Extinct) ln-transformed Model box plots of Fossil Hominin predicted $M_1$Age (years).

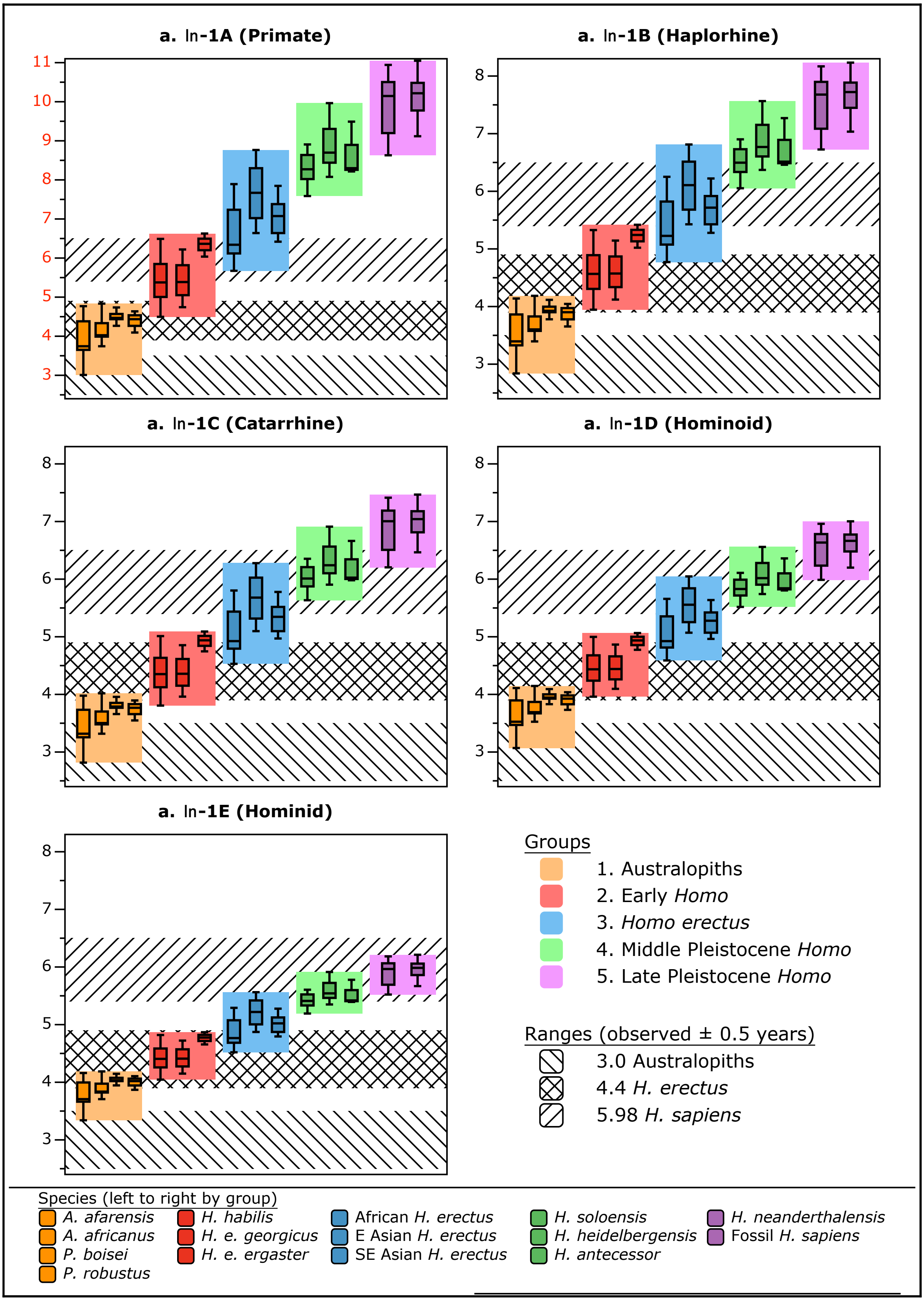

**Figure 9.3.** **Box & Whisker Plots: ln-Models, Set 1**
Comparison of Set 1 (Extant Only) ln-transformed Models box plots of Fossil Hominin predicted $M_1$Age (years).

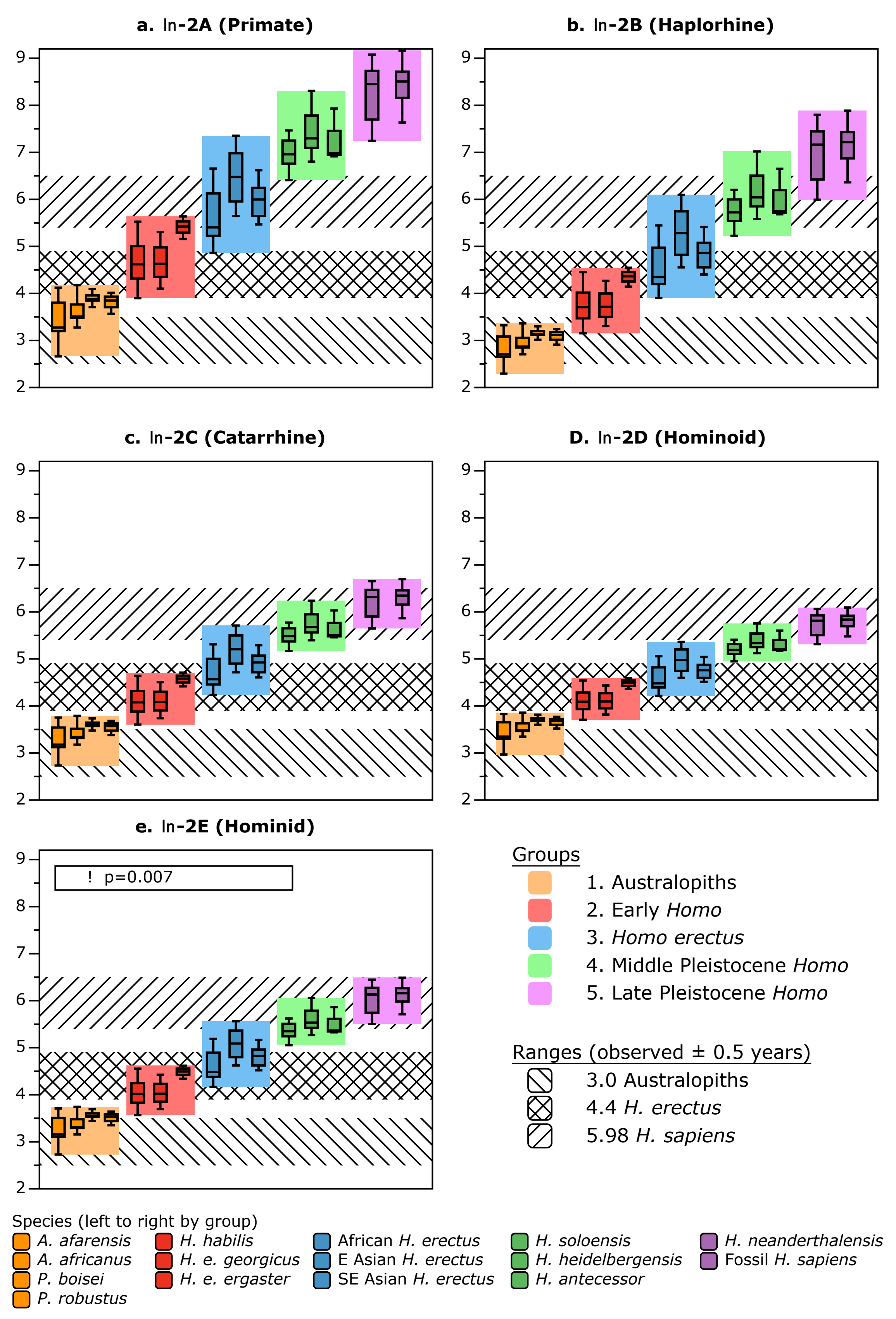

**FIGURE 9.4. BOX & WHISKER PLOTS: ln-MODELS: SET 2**
Comparison of Set 2 (Extant & Extinct) ln-transformed Models box plots of Fossil Hominin predicted $M_1$Age (years).

# Appendix 6. Cubic Models

## Appendix 6.a. Cubic Models: Tables

| **SET 1. EXTANT ONLY** | |
|---|---|
| 1A. Primate | $y = 0.06575+ 0.01617x - 0.00002207x^2 + 0.000000009844x^3$ |
| 1B. Haplorhine | $y = 0.1891 + 0.01479x - 0.00001874x^2 + 0.000000008091x^3$ |
| 1C. Catarrhine | $y = 0.3216 + 0.01328x - 0.00001514x^2 + 0.000000006195x^3$ |
| 1D. Hominoid | $y = -0.5992 + 0.02875x - 0.00005513x^2 + 0.00000002771x^3$ |
| 1E. Hominid | $y = 4.3850 - 0.000005785x^2 + 0.000000004903x^3$ |
| **SET 2. EXTANT & EXTINCT** | |
| 2A. Primate | $y = 0.05623 + 0.01675x - 0.00002657x^2 + 0.00000001266x^3$ |
| 2B. Haplorhine | $y = 0.1888 + 0.01607x - 0.00002554x^2 + 0.000000012224x^3$ |
| 2C. Catarrhine | $y = 0.3162 + 0.01494x - 0.00002324x^2 + 0.00000001112x^3$ |
| 2D. Hominoid | $y = 0.8925 + 0.01390x - 0.00002393x^2 + 0.00000001192x^3$ |
| 2E. Hominid | $y = 8.1318 - 0.01736x + 0.00001637x^2 - 0.0000000035x^3$ |

**TABLE 9.16 CUBIC MODELS: EQUATIONS**

| | SET 1 (EXTANT ONLY) | | | | SET 2 (EXTANT & EXTINCT) | | |
|---|---|---|---|---|---|---|---|
| | R | P | Se | | R | P | Se |
| A. Primate | 0.97 | < 0.001 | 0.318 | | 0.95 | < 0.001 | 0.482 |
| B. Haplorhine | 0.97 | < 0.001 | 0.372 | | 0.96 | < 0.001 | 0.460 |
| C. Catarrhine | 0.95 | < 0.001 | 0.457 | | 0.94 | < 0.001 | 0.534 |
| D. Hominoid | 0.96 | = 0.034 | 0.616 | | 0.93 | < 0.001 | 0.627 |
| E. Hominid | 0.87 | = 0.488 | 1.048 | | 0.95 | = 0.005 | 0.554 |

**TABLE 9.17 CUBIC MODELS: SUMMARIES**

| CUBIC MODELS, PREDICTED $M_1$AGE (YEARS) | | | | | | | |
|---|---|---|---|---|---|---|---|
| | **1A** | **1B** | **1C** | **—** | **—** | **—** | **—** |
| *H. erectus* | 3.9 | 4.2 | 4.6 | — | — | — | — |
| *H. sapiens* | 5.90 | 5.90 | 5.90 | — | — | — | — |
| *P. troglodytes* | 3.51 | 3.48 | 3.45 | — | — | — | — |
| Fossil *H. Sapiens* | 7.67 | 7.3 | 7.0 | — | — | — | — |
| *H. neanderthalensis* | 7.13 | 6.9 | 6.6 | — | — | — | — |
| Australopiths | 3.84 | 3.8 | 3.9 | — | — | — | — |

**TABLE 9.18 CUBIC MODELS, SET 1: PREDICTED $M_1$AGE**

Comparison table of Cubic Models, predicted $M_1$Age (years). Comparison table of ln-transformed models: predicted $M_1$Age (years). Because the stage one criteria is not met, Cubic-1D and Cubic-1E were not used for predictions. Quadratic equations were a better fit for Set 2 predictions.

## Appendix 6.b. Cubic Models: Figures

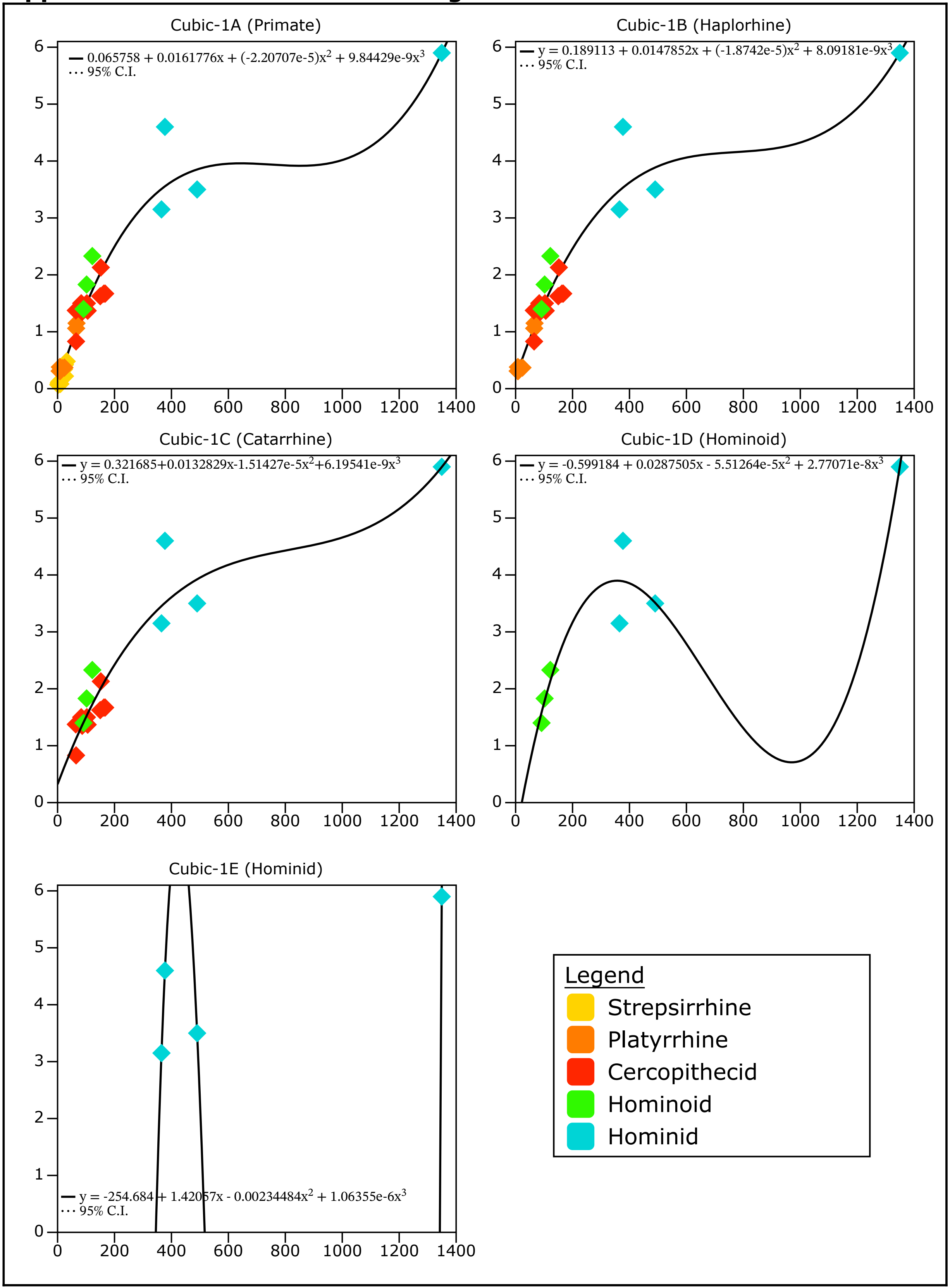

**Figure 9.5. Regression Plots: Cubic Models, Set 1**
Comparison of Set 1 (Extant Only) Cubic Model scatterplots.

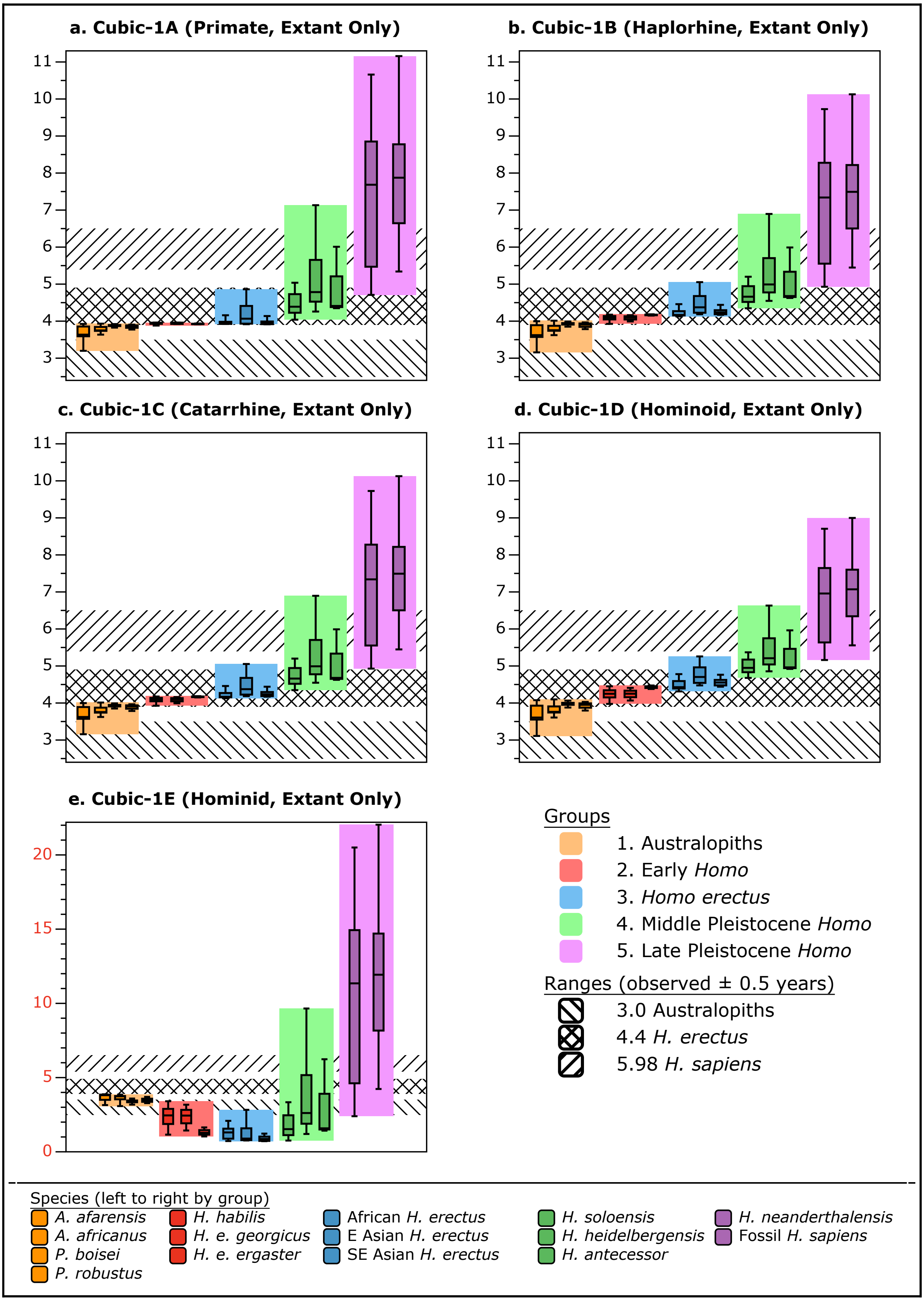

**FIGURE 9.6.** **BOX & WHISKER PLOTS: CUBIC MODELS, SET 1**
Comparison of Set 1 (Extant Only) Cubic Model box plots of Fossil Hominin predicted $M_1$Age (years).

# Appendix 7. Quadratic Models

## Appendix 7.a. Quadratic Models: Tables

| **Set 1. Extant Only** | |
|---|---|
| 1A. Primate | $y = 0.2597 + 0.01099x - 0.000005092x^2$ |
| 1B. Haplorhine | $y = 0.4320 + 0.01007x - 0.000004487x^2$ |
| 1C. Catarrhine | $y = 0.6673 + 0.00883x - 0.000003679x^2$ |
| 1D. Hominoid | $y = 1.1320 + 0.00755x - 0.000002989x^2$ |
| 1E. Hominid | $y = 5.4870 - 0.006265x + 0.000004868x^2$ |
| **Set 2. Extant & Extinct** | |
| 2A. Primate | $y = 0.4509 + 0.008103x - 0.000002839x^2$ |
| 2B. Haplorhine | $y = 0.7147 + 0.007018x - 0.000002185x^2$ |
| 2C. Catarrhine | $y = 1.1187 + 0.005404x - 0.000001221x^2$ |
| 2D. Hominoid | $y = 1.9238 + 0.003034x - 0.00000006071x^2$ |
| 2E. Hominid | $y = 6.8344 - 0.011289x + 0.00000775x^2$ |

**Table 9.19 Quadratic Models: Equations**

| | **Set 1 (Extant Only)** | | | **Set 2 (Extant & Extinct)** | | |
|---|---|---|---|---|---|---|
| | **R** | **P** | ***Se*** | **R** | **P** | ***Se*** |
| A. Primate | 0.97 | $< 0.001$ | 0.364 | 0.93 | $< 0.001$ | 0.589 |
| B. Haplorhine | 0.96 | $< 0.001$ | 0.396 | 0.94 | $< 0.001$ | 0.577 |
| C. Catarrhine | 0.95 | $< 0.001$ | 0.449 | 0.93 | $< 0.001$ | 0.592 |
| D. Hominoid | 0.94 | $= 0.015$ | 0.680 | 0.90 | $< 0.001$ | 0.699 |
| E. Hominid | 0.87 | $= 0.490$ | 1.053 | 0.95 | $< 0.001$ | 0.508 |

**Table 9.20 Quadratic Models: Summaries**

| **Quadratic Models: Predicted $M_1$Age (years)** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **—** | **—** | **—** | **2A** | **2B** | **2C** | **2D** | **2E** |
| *H. erectus* | — | — | — | 5.6 | 5.4 | 5.1 | 4.7 | 3.1 |
| *H. sapiens* | — | — | — | 6.2 | 6.2 | 6.2 | 5.9 | 5.8 |
| *P. troglodytes* | — | — | — | 3.0 | 3.0 | 2.9 | 3.0 | 3.8 |
| Fossil *H. Sapiens* | — | — | — | 6.2 | 6.3 | 6.5 | 6.3 | 7.2 |
| *H. neanderthalensis* | — | — | — | 6.2 | 6.3 | 6.4 | 6.2 | 6.8 |
| Australopiths | — | — | — | 3.7 | 3.6 | 3.5 | 3.4 | 3.2 |

**Quadratic Models: Set 2: Predicted $M_1$Age**
Comparison table of Set 2 (Extant & Extinct) Quadratic Models predicted $M_1$Age (years). Quadratic equations were not used for predictions with the Set 1 groups because Cubic Models were a better fit.

## Appendix 7.b. Quadratic Models: Figures

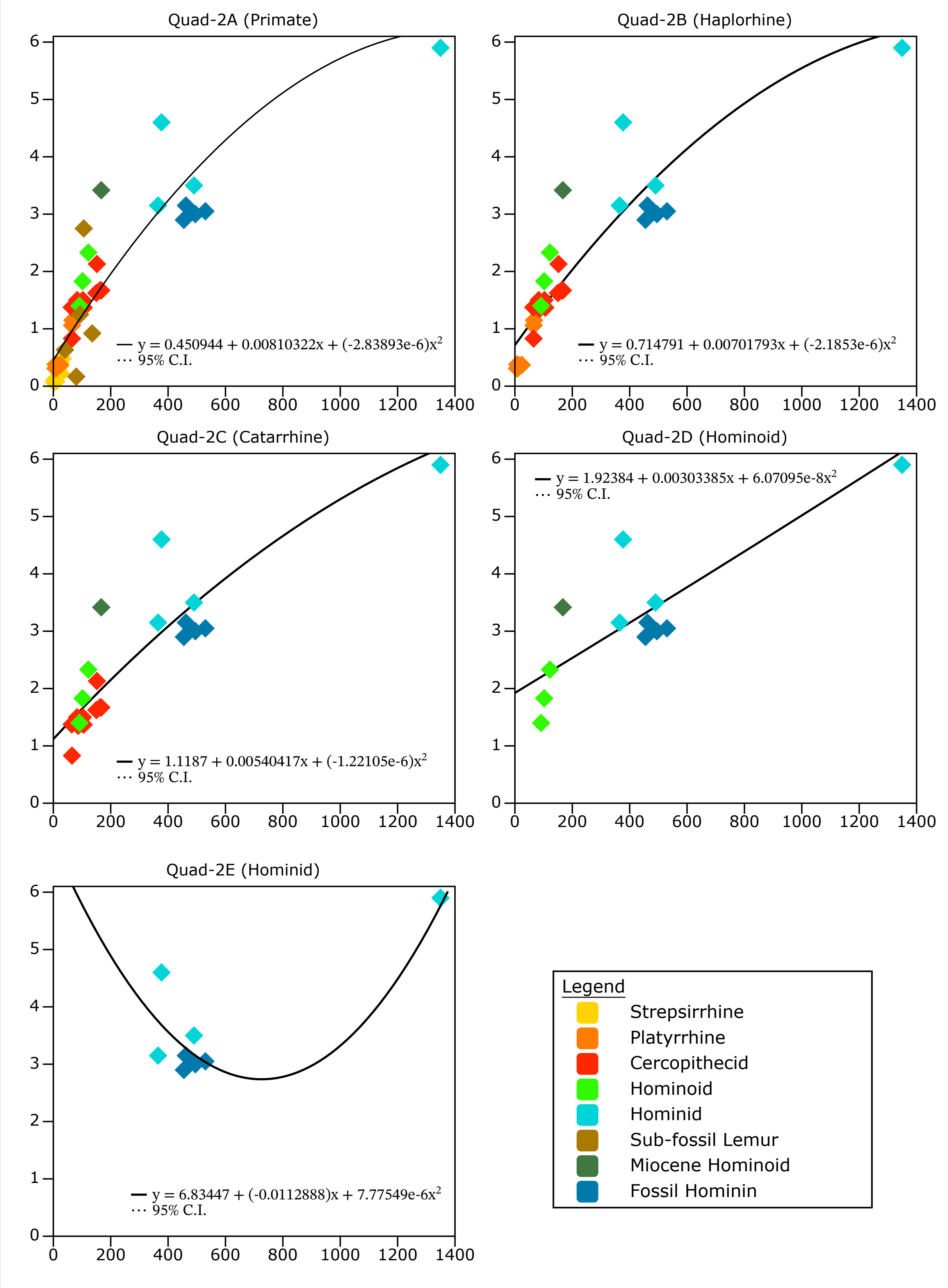

**FIGURE 9.7. REGRESSION PLOTS: QUADRATIC MODELS, SET 2**
Comparison of Set 2 (Extant & Extinct) Quadratic model regression scatterplots. Note this equation plots as nearly linear, with no visual curve characteristic of second degree polynomial equations. e. Note the inverted curve on this equation.

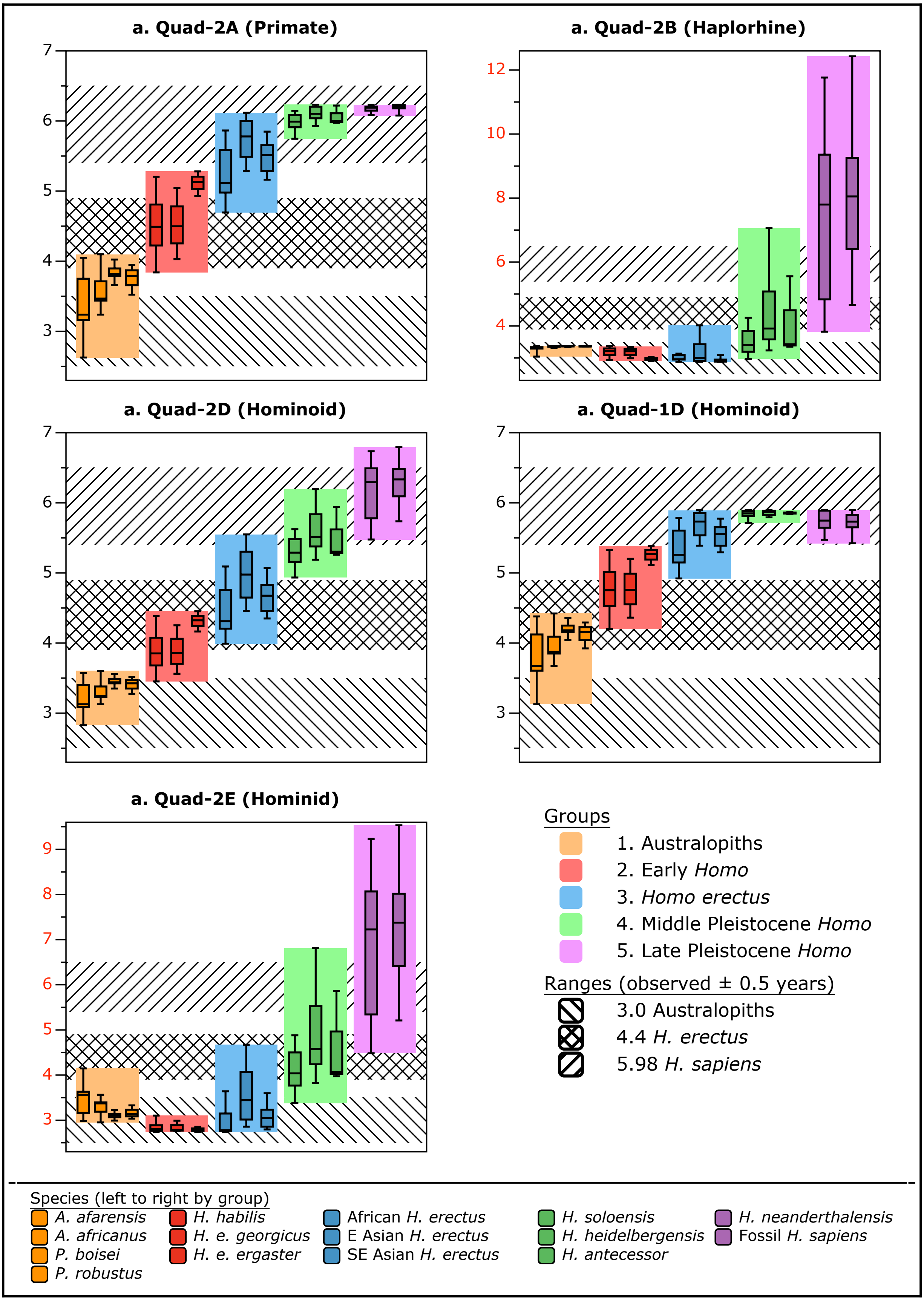

**Figure 9.8.** **Box & Whisker Plots: Quadratic Models, Set 2**

Comparison of Set 2 (Extant & Extinct) Quadratic Model box plots of Fossil Hominin predicted $M_1$Age (years).

# Appendix 8. Linear Models

## Appendix 8.a. Linear Models: Tables

| | |
|---|---|
| **SET 1. EXTANT ONLY** | |
| 1A. Primate | $y = 0.6929 + 0.004803x$ |
| 1B. Haplorhine | $y = 0.9644 + 0.004376x$ |
| 1C. Catarrhine | $y = 1.3037 + 0.003857x$ |
| 1D. Hominoid | $y = 1.1953 + 0.003211x$ |
| 1E. Hominid | $y = 2.8504 + 0.002226x$ |
| **SET 2. EXTANT & EXTINCT** | |
| 2A. Primate | $y = 0.7752 + 0.004495x$ |
| 2B. Haplorhine | $y = 1.0624 + 0.004108x$ |
| 2C. Catarrhine | $y = 1.3933 + 0.003673x$ |
| 2D. Hominoid | $y = 1.9022 + 0.003128x$ |
| 2E. Hominid | $y = 1.9893 + 0.003021x$ |

**TABLE 9.21 LINEAR MODELS: EQUATIONS**

| | SET 1 (EXTANT ONLY) | | | | SET 2 (EXTANT & EXTINCT) | | |
|---|---|---|---|---|---|---|---|
| | R | P | Se | | R | P | Se |
| A. Primate | 0.88 | < 0.001 | 0.770 | | 0.89 | < 0.001 | 0.702 |
| B. Haplorhine | 0.89 | < 0.001 | 0.642 | | 0.91 | < 0.001 | 0.661 |
| C. Catarrhine | 0.90 | < 0.001 | 0.607 | | 0.92 | < 0.001 | 0.608 |
| D. Hominoid | 0.89 | = 0.007 | 0.790 | | 0.90 | < 0.001 | 0.666 |
| E. Hominid | 0.85 | = 0.151 | 0.803 | | 0.90 | = 0.001 | 0.666 |

**TABLE 9.22 LINEAR MODELS: SUMMARIES**

| ln-TRANSFORMED MODELS: PREDICTED $M_1$AGE (YEARS) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **1A** | **1B** | **1C** | **2A** | **2B** | **2C** | **2D** | **2E** |
| *H. erectus* | 5.2 | 5.2 | 4.9 | 5.0 | 4.9 | 4.8 | 4.8 | 4.8 |
| *H. sapiens* | 7.2 | 6.9 | 6.5 | 6.8 | 6.6 | 6.4 | 6.1 | 6.1 |
| *P. troglodytes* | 2.5 | 2.6 | 2.7 | 2.4 | 2.6 | 2.7 | 3.0 | 3.1 |
| Fossil *H. Sapiens* | 7.8 | 7.5 | 7.0 | 7.5 | 7.2 | 6.9 | 6.6 | 6.5 |
| *H. neanderthalensis* | 7.7 | 7.3 | 6.9 | 7.3 | 7.0 | 6.7 | 6.4 | 6.4 |
| Australopiths | 3.0 | 3.1 | 3.2 | 3.0 | 3.1 | 3.2 | 3.4 | 3.5 |

**TABLE 9.23 LINEAR MODELS: PREDICTED $M_1$AGE**
Comparison table of Linear models, predicted $M_1$Age (years). Because the stage one criteria is not met, Linear-1D and Linear-1E were not used for predictions.

## Appendix 8.b. Linear Models: Figures

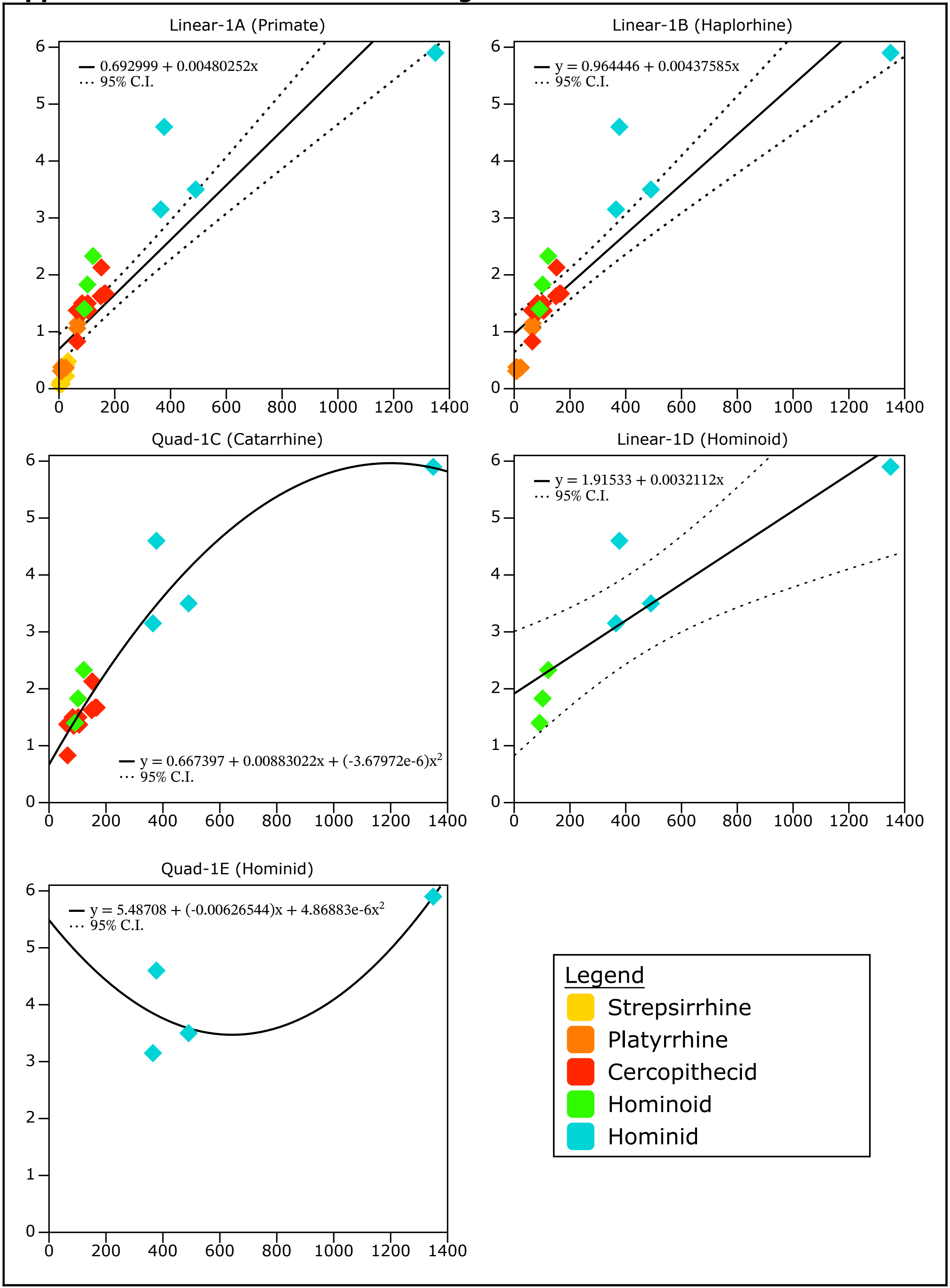

**FIGURE 9.9. REGRESSION PLOT: LINEAR MODELS: SET 1**
Comparison of the Set 1 (Extant Only) Linear models regression scatterplots.

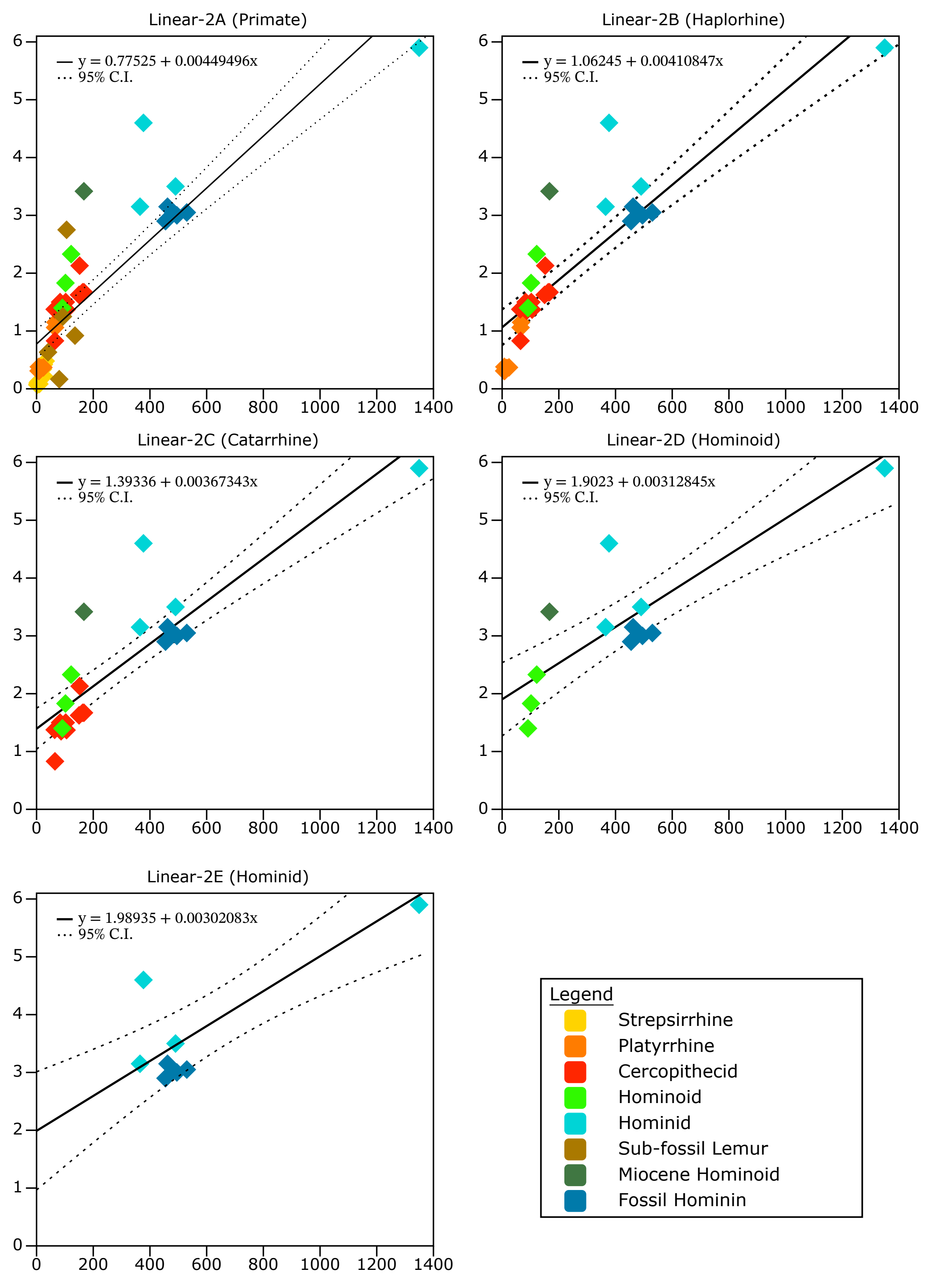

**FIGURE 9.10.** **REGRESSION PLOTS: LINEAR MODELS, SET 2**
Comparison of the Set 2 (Extant & Extinct) Linear Models regression scatterplots.

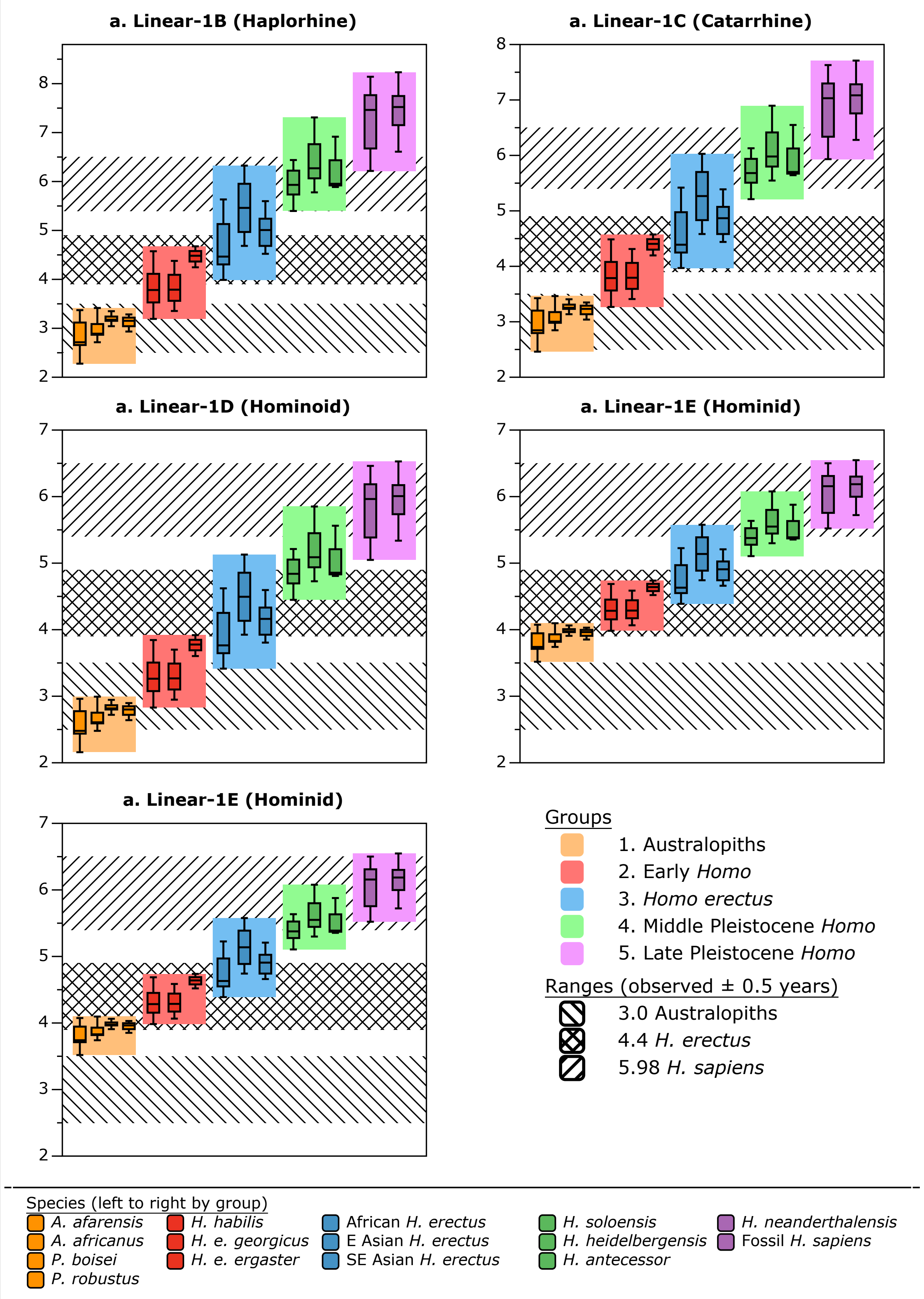

**Figure 9.11. Box & Whisker Plots: Linear Models, Set 1**
Comparison of Set 1 (Extant Only) Linear Model box plots of Fossil Hominin predicted $M_1$Age (years).

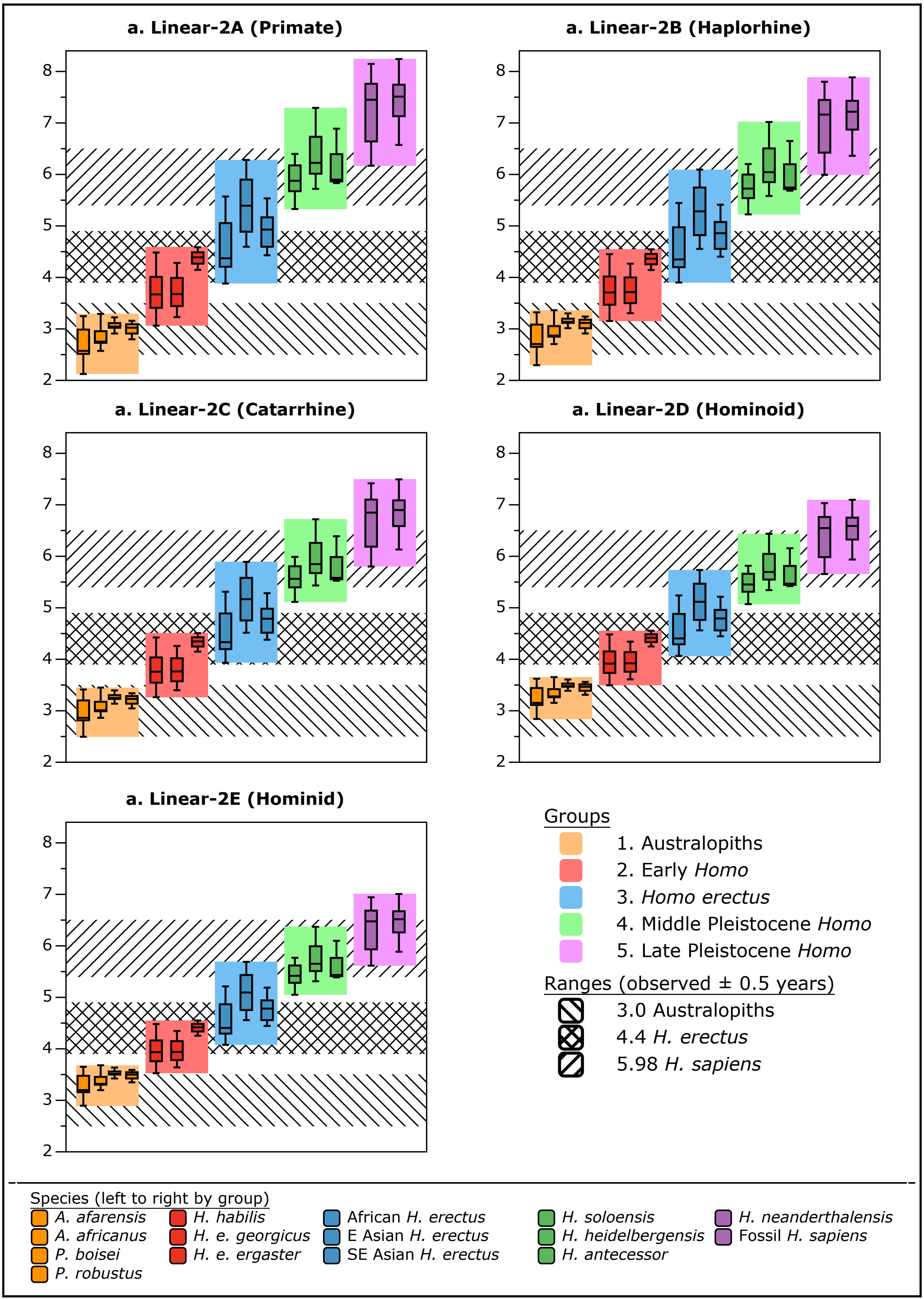

**FIGURE 9.12. BOX & WHISKER PLOTS: LINEAR MODELS, SET 2**
Comparison of Set 2 (Extant & Extinct) Linear Model box plots of Fossil Hominin predicted $M_1$Age (years).

# List of Abbreviated Terms

AC = accuracy criteria (observed $M_1$Age ± 0.2 yr)

AFR = age of first reproduction (generally this is female unless otherwise noted)

AMH = anatomically modern human(s)

BW = birth weight

CF = complementary feeding (supplementary foods consumed by infant which supplements nutrition from suckling)

ECV = endocranial volume (in ml)

IBI = interbirth interval (in years)

$\ln - \ln =$ two-sided $\ln$-transformed model

LHV = life history variable

LHRV = life history related variable

life span = maximum recorded life span for a species

$M_1$Age = age of emergence of lower 1st permanent molar (in years)

MVT = Movius Line Theory

RC = range criteria (= observed $M_1$Age ± 0.5 yr; see Section 4.2.4 above)

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