

## Chapter 31. *Paranthropus* growth and life history: toward a primate perspective

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### INTRODUCTION

Life history research in living organisms seeks to explain the varied strategies for the allocation of energetic and other resources throughout a species' lifetime, especially with respect to growth, maturity and reproduction (Clutton-Brock and Harvey, 1985; Smith, 1989a; Leigh and Blomquist, 2007). Life history is usually conceptualized as a series of life phases that ultimately relate to scheduling reproduction and maximising lifetime reproductive output (Kelley, 2002; Kelley and Smith, 2003). Life history traits (or variables) are those observable and measurable species characteristics that relate to the timing and pattern of growth, development to maturity, maintenance of body structures, metabolic rate, and reproduction. The different ways that such traits are combined can be described in relation to species' adaptive strategies, and this involves the concept of trade-offs (Jones, 2011; Ross, 1998; Stearns, 1989). Since available energy is limited for all species not all traits can be maximized by selection at once; the energy allocated to one variable cannot simultaneously be made available to others. One implication of this perspective is that variation in life history among species – i.e., in the pattern and timing of growth processes and maturation events – can be understood in relation to variation in morphology, behaviour, ecology and reproductive strategy in an evolutionary context (DeRousseau, 1990; Harvey et al., 1986; Stearns, 1992).

Life history research in living primates can incorporate data on a wide range of life history variables, but such studies seldom include data about dental development or skeletal maturation (Godfrey et al., 2001), which are difficult to observe in field studies (Smith, et al., 2013). In contrast, due to the abundance of dental specimens in the fossil record, life history research in palaeoanthropology relies heavily on different aspects of dental development (especially age at M1 emergence; see below) and dental microstructure (Dean, 1987, 2000, 2006; Smith, 2013; Smith et al. 2015) to reconstruct the overall schedule and details of timing of (dental) life history variables (Godfrey et al., 2001; Kelley and Smith, 2003; Dirks and Bowman, 2007; Kelley and Schwartz, 2010). Most other aspects of life history cannot be directly observed in extinct species, but in theory some can be inferred on the basis of comparative studies.

In a historical context, one of the key questions in palaeoanthropology has been about the evolutionary origins of the prolonged period of growth and development in modern humans, which has long been considered essential for our culture, intelligence, language and other 'human-like' traits (e.g., Dobzhansky, 1962; Isaac, 1972; Mann, 1975). Earlier research on life history in extinct hominins largely involved assessing the scheduling and duration of growth and development along the 'fast-slow continuum' (Kelley, 1997; Smith & Tompkins, 1995; Smith, 1992), and determining when the prolonged, slow human life history pattern evolved. Thus, until recently life history studies in palaeoanthropology generally utilised a comparative framework between 'ape' (usually represented by *Pan troglodytes*) and 'human'

trait conditions, and characterising early hominins according to any similarity with either to infer the timing of growth in extinct hominins (Bromage, 1987a; Bromage & Dean, 1985a; Conroy & Kuykendall, 1995; Conroy & Vannier, 1991a; Smith, 1994).

It is now widely accepted that the life history schedule in early hominins, including *Australopithecus*, *Paranthropus*, and early *Homo*, was short and thus more similar to that of extant apes (Smith, 1986, 1989a, 1989b; Bromage and Dean, 1985; Bromage, 1987; Beynon and Dean, 1988). In addition, there is now compelling evidence that life history schedules and different aspects of growth, while similar in the overall period of growth and maturation, varied significantly between early hominin species (Beynon & Dean, 1988; Bromage, 1987a; Bromage & Dean, 1985a; Conroy, 1988; Conroy & Vannier, 1987, 1991a; Dean, 1985a; Kelley & Schwartz, 2012; Kuykendall, 2003); the pattern and timing of life history in extinct hominins is not equivalent to that in either extant apes or humans. Overall, the evolution of life history strategies among extinct and extant hominins and apes is more nuanced than can be represented by the ‘fast-slow continuum’. To add to this complexity, more recent research on wild populations of *Pan* (Boughner & Dean, 2008; Kelley, Schwartz, & Smith, 2014; Machanda et al., 2015; Smith, Machanda, et al., 2013; Walker, Walker, Goodall, & Pusey, 2018), *Gorilla* (Breuer et al., 2009; Galbany et al., 2017; Kralick et al., 2017; Stoinski et al., 2013) and *Pongo* (Smith, 2016; van Noordwijk et al., 2018; Wich et al., 2004) have documented that a considerable degree of life history variation exists among extant hominoids – what exactly is an ‘ape-like’ life history?

The observed variation in the pattern and timing of life history among extant apes – and by inference, that among extinct hominin species – can be explained in part by differences in factors such as ecological conditions, energy expenditure and basal metabolic rate (Pontzer, 2017), as well as strategies for risk aversion (Janson & van Schaik, 1993) but the details of such relationships are often speculative.

These issues present a challenge for research – how can we tease out evidence of such details of life history variation among extinct hominins when the primary source of data is still composed of a fragmentary dental, gnathic and (sometimes) cranial fossil assemblage? It remains the case that extant and extinct primate life history data sets usually do not share key variables needed (Godfrey et al., 2001). While new technology and approaches demonstrate great potential to further illuminate our understanding of variation in dental development and life history timing (Dean, Liversidge, & Elamin, 2014; Dean, 1987; Lacruz, Ramirez Rozzi, & Bromage, 2006; Smith et al., 2015), it has also been demonstrated that broader questions about early hominin life history can be approached by continued exploration of the factors associated with life history variation in extant primates (Catlett, Schwartz, Godfrey, & Jungers, 2010; Godfrey et al., 2001; Kelley & Schwartz, 2010; Lee, 2012; Macho, 2014; 2015). Exploration of this broad-level approach to life history reconstruction in extinct hominins is one aim of this contribution.

### ***Why Paranthropus?***

The genus *Paranthropus* refers to the ‘robust australopiths’ (Constantino, 2013), first discovered and described from Kromdraai in South Africa (Broom, 1938). In addition to the Kromdraai fossils, fossils attributed to *P. robustus* were recovered from Swartkrans (Broom, 1948; Broom & Robinson, 1952), and in 1959 *Zinjanthropus* (now *Paranthropus*) *boisei* was

recovered from Olduvai Gorge in Tanzania (Leakey, 1959). Additional fossils attributed to *P. boisei* have been reported from sites in Kenya, Ethiopia, and Malawi (Kullmer et al., 1999; Wood & Constantino, 2007), and a third species, *P. aethiopicus* is known from Kenya and Ethiopia (Walker, Leakey, Harris, & Brown, 1986). Thus, at least two species of *Paranthropus* are comparatively well-known from the fossil record of East and South Africa between about 2.6 and 1.0 Ma (Wood & Richmond, 2000; Wood & Constantino, 2007).

Palaeo-environmental and habitat reconstructions for *Paranthropus* species in East and South Africa are variable (Wood & Constantino, 2007; Wood & Strait, 2004). *Paranthropus* fossils have been recovered at sites that generally represent open habitats, but closed habitats are also represented. The key feature is the presence of permanent water sources, and *Paranthropus* habitats include edaphic grasslands and wetlands (Reed, 1997; Wood & Strait, 2004). Different site habitat reconstructions at sites where *Paranthropus* fossils have been recovered range from grassland to open bushland or woodland and include deltaic and lake margin habitats. Sites in East Africa (*P. boisei*) are characterized as wetter with more closed habitats, and those in South Africa (*P. robustus*) are described as drier with more open grasslands (Grine, Sponheimer, et al., 2012; Reed, 1997; Wood & Strait, 2004). While other early hominins also occupied mosaic and widely varying habitats (Behrensmeyer & Reed, 2008), the range of habitats associated with *Paranthropus* fossils appears to have been unique among hominins and the open habitats would have presented conditions – e.g., increased predator risk, and both dispersed and lower-quality diet resources - affecting life history strategies in varied ways among populations of *Paranthropus* throughout its geographic range.

Compared to the size range among all primates, the species of *Paranthropus* are characterized by relatively large brain and body sizes, similar to extant apes and to other early hominins. However, they are clearly distinguished from such early hominins of the genera *Australopithecus* and *Homo* by their prominent bony attachments for chewing muscles, the large size and robusticity of the mandible, the large and thick-enamelled post-canine dentition, and other traits (McCullum, 2008; Wood & Richmond, 2000; Wood, 1992; Wood & Constantino, 2007). These distinctions in *Paranthropus* morphology, and the adaptive and behavioural inferences that have been drawn from them may be a reflection of *Paranthropus* life history. What do the morphological and adaptive differences between *Paranthropus* and other extinct hominins imply about variation in life history strategies?

Robinson's Dietary Hypothesis (Robinson, 1963) has been a long-standing explanatory model relating differences in morphology to variation in dietary adaptations between *Paranthropus* and more gracile species of *Australopithecus* and early *Homo*. Conventional interpretations of the robust masticatory structures in *Paranthropus* relate to a unique dietary adaptation for either hard or fibrous food items requiring heavy mastication and producing increased occlusal loads. Research incorporating biomechanics (Smith et al., 2015; Strait et al., 2012; Wood & Strait, 2004), dental microwear (Frederick E. Grine, Sponheimer, et al., 2012; Peterson et al., 2018; Ungar et al., 2008, 2011), stable isotopes (Cerling et al., 2011; Lee-Thorp, et al., 2010; Sponheimer et al., 2006) and fallback foods (Constantino & Wright, 2009; Laden & Wrangham, 2005; Ungar et al., 2008) has attempted to clarify the dietary differences between *Paranthropus* and other early hominins. Recent research demonstrating unexpected similarity in patterns of complexity and anisotropy in dental microwear and stable isotope signatures (Scott et al., 2005; Sponheimer et al., 2013) has resulted in a re-evaluation

of early hominin diet reconstructions, and a sound rejection of the ‘Nutcracker Man’ model for *Paranthropus* diet (Lee-Thorp, 2011). At the very least, this reflects a consensus that dietary reconstruction among early hominins is more complex and uncertain than historically recognized. Stable isotope studies indicate that *P. robustus* was a C3-feeder (foliage and browse) with a variable C4-component to the diet (Sponheimer et al., 2006), and *P. boisei* was a C4 (grasses, sedges) consumer unlike any other early hominin (Cerling et al., 2011; Grine et al., 2012; Van Der Merwe et al., 2008). These isotopic characterisations of *Paranthropus* diets are not immediately consistent with the habitat reconstructions for South (open, drier) and East (closed, wetter) African habitat reconstructions noted above. Diet is a key variable in understanding growth and life history variation (Dirks & Bowman, 2007; Godfrey, Samonds, Jungers, Sutherland, & Irwin, 2004; Leigh, 1994; Macho & Williamson, 2002) and these unexpected aspects of diet variation in *Paranthropus* should be evaluated in the broad context of life history variation among primates and other mammals.

Like other early hominins, *Paranthropus* exhibits sex dimorphism in body size and cranial morphology (Kimbel & White, 1988; Lockwood et al., 2007; McHenry, 1992). Sex dimorphism may have consequences for variation in developmental timing in males and females (Leigh, 1992; Leigh & Shea, 1995; Shea, 1986), and thus should be considered in life history reconstruction. In addition, in cases of extreme sex dimorphism such as *Gorilla* and *Pongo*, males may demonstrate much later cessation of growth compared to females (bimaturism), associated with attainment of social dominance as an adult (Shea, 1985; Utami, 2002). In extant primates, high levels of sex dimorphism, sometimes involving bimaturism, are commonly associated with high levels of male-male competition (Plavcan & Van Schaik, 1997) and other social and ecological factors (Leigh, 1995; Leigh & Shea, 1996), including infanticide (Breuer et al., 2009). Normally, these features are associated with strong sex dimorphism in canine crown size, which is uniquely absent in *Paranthropus*. These factors also have implications for understanding life history variation in *Paranthropus* but are largely absent in the existing literature.

As the genus name implies (roughly translated as ‘to the side of Man’), *Paranthropus* is thought to be an extinct ‘side branch’ of hominin phylogeny. While comparisons with *Australopithecus* and *Homo* are inevitable, *Paranthropus* presents an opportunity to explore factors affecting variation and constraint of life history in a divergent subclade of hominins (Skinner & Wood, 2006), and beyond the ‘chimpanzee-human’ dichotomy commonly utilized. Thus, while recognising its taxonomic status as a hominin, the question in this approach could be phrased, ‘In terms of life history variation, what kind of primate was *Paranthropus*?’

The first part of this paper aims to review and synthesize past research about *Paranthropus* life history, dental development, and other aspects of growth in comparison to other extinct hominins and to extant apes. The discussion will present a broad consideration of growth and life history research in living primates with the aim to further illuminate our reconstructions of *Paranthropus* adaptation and palaeobiology.

## RECONSTRUCTING *PARANTHROPUS* LIFE HISTORY

### The *Paranthropus* juvenile fossil assemblage

Before addressing research to reconstruct growth and life history in *Paranthropus*, it is worth considering the nature of the available juvenile fossil assemblage on which such research is based (Table 31.1). This table compiles information about those specimens commonly utilised in research about dental maturation and life history but does not attempt to list all juvenile *Paranthropus* specimens published. Additional new juvenile material has been reported (Keyser, et al., 2000; Moggi-Cecchi, et al., 2010; Pickering et al., 2012, 2016) and consists largely of fragmentary dento-gnathic specimens and isolated permanent and deciduous teeth.

Overall, the assemblage of juvenile *Paranthropus* fossils is dominated by teeth and jaws, and notably lacks partial or relatively complete cranial specimens, such as Dikika (*Au. afarensis*) (Alemseged et al. 2006) or Taung (*Au. africanus*) (Dart, 1925). In addition, there is a lack of associated juvenile skeletons or isolated postcranial material, such as the KNM-WT 15000 Nariokotome Boy (Brown, et al., 1985; Walker and Leakey, 1993) or MH-1 *Australopithecus sediba* (Berger et al., 2010; Cameron et al. 2017) skeletons, both of which have been the subject of growth assessments. (The juvenile *Paranthropus* specimen DNH 44 listed by Keyser et al. (2000) includes a mandible fragment with dentition and a right ulna; the mandible and teeth were included in T. Smith et al., (2015). In addition, Cazenave et al., (2020) recently re-assessed the fragmentary TM1517 (type specimen) juvenile. Thus, even more critically than for other early hominin species, what we currently understood about *Paranthropus* growth and life history is derived from developing hard tissues of the dentition and jaws.

Table 31.1 (see also Table 31.3) demonstrates that the *Paranthropus* immature fossil assemblage includes a high proportion of very young individuals (based on the presence of mixed dentitions and estimates for age-at-death), particularly for *P. robustus* in South Africa. If this observation reflects a *Paranthropus* mortality profile (Bromage, 1990; Bromage & Dean, 1985; Mann, 1975; McKinley, 1971; Shaaban, 2002; Tobias, 1999), and not taphonomic bias (Chamberlain, 2006), it would suggest the impact of one or more environmental risk factors relevant to life history reconstructions. These perspectives are considered further in the discussion.

<INSERT TABLE 31.1 ABOUT HERE: the *Paranthropus* juvenile fossil assemblage>

Table 31.1. The *Paranthropus* immature fossil assemblage. This table lists a sample of immature fossil specimens that have been reported in research papers about growth, dental development and life history in early hominins. Isolated teeth are generally not included, except where incremental data has produced an estimated age at death. It is not meant to be a comprehensive list of all *Paranthropus* immature material recovered, as some of the available specimens may not have been incorporated into such studies (see Braga et al., 2017; Moggi-Cecchi et al., 2010; Pickering et al., 2012, 2016). Some specimens listed were also included in earlier publications such as Mann (1975) and Skinner and Sperber (1982). Where available for specimens listed, estimated ages at death are presented in Table 31.3. See text for additional comments. DNH = Drimolen, OH = Olduvai Gorge, KNM-ER = Koobi Fora, SK/SKX/SKW/EM = Swartkrans, TM/KB = Kromdraai.

| Specimen           | Species            | Description  | Key References   |
|--------------------|--------------------|--|--|
| <b>KNM-ER 1477</b> | <i>P. boisei</i>   | right and left mandibular corpora with deciduous teeth and developing permanent tooth crowns | Bromage & Dean, 1985; Dean, 1987a; Beynon & Dean, 1988; Aiello et al 1991; T. Smith, 2008    |
| <b>KNM-ER 1820</b> | <i>P. boisei</i>   | partial left mandibular corpus with deciduous teeth and developing permanent tooth crowns    | Dean, 1987a; Beynon & Dean, 1988; Aiello et al 1991; T. Smith, 2008; Kelley & Schwartz, 2012 |
| <b>KNM-ER 812</b>  | <i>P. boisei</i>   | left mandibular corpus with deciduous teeth and developing permanent tooth crowns            | Dean, 1987a; Beynon & Dean, 1988; T. Smith, 2008   |
| <b>OH 5</b>        | <i>P. boisei</i>   | Partial cranium with M3 roots incomplete   | Beynon & Dean, 1988  |
| <b>OH 30</b>       | <i>P. boisei</i>   | associated isolated mixed dentition including maxillary and mandibular teeth                 | Dean, 1987a; Beynon & Dean, 1988; T. Smith, 2008   |
| <b>OMO-L-427-7</b> | <i>P. boisei</i>   | Partial mandible with M1 and developing PM4 and M2 crowns                                    | Beynon & Dean, 1988  |
| <b>WT 17400</b>    | <i>P. boisei</i>   | Maxilla with associated permanent teeth and developing M3 crown                              | Beynon & Dean, 1988  |
| <b>DNH 101</b>     | <i>P. robustus</i> | isolated R mandibular M2   | Smith, T. et al. 2015  |
| <b>DNH 107</b>     | <i>P. robustus</i> | associated teeth including R mandibular I1, C, M1  | Smith, T. et al. 2015  |

|                       |                    |  |   |
|-----------------------|--------------------|--|---|
| <b>DNH 108</b>        | <i>P. robustus</i> | associated teeth including L maxillary C, P3, M1 and R maxillary C, P3, M1, M2   | Smith, T. et al. 2015   |
| <b>DNH 44</b>         | <i>P. robustus</i> | partial right mandibular corpus with deciduous teeth in occlusion and M1 in crypt  | Smith, T. et al. 2015   |
| <b>DNH 47</b>         | <i>P. robustus</i> | partial maxilla with L dP4, M1 and R I1  | Smith, T. et al. 2015   |
| <b>DNH 60</b>         | <i>P. robustus</i> | cranial fragments with associated deciduous teeth and developing permanent tooth crowns including L maxillary M1 and R mandibular M1, M2 | Smith, T. et al. 2015   |
| <b>DNH 84</b>         | <i>P. robustus</i> | maxilla with R I1 and LI1, M1  | Smith, T. et al. 2015   |
| <b>SK 13</b>          | <i>P. robustus</i> | maxilla with incomplete permanent dentition  | Mann 1975; Bromage 1987; Braga 1998   |
| <b>SK 1587</b>        | <i>P. robustus</i> | partial mandible with partially emerged permanent dentition  | Cofran, 2014  |
| <b>SK 25</b>          | <i>P. robustus</i> | Mandible with dm2 and developing permanent molars  | Bromage 1987; Beynon & Dean, 1988; Cofran, 2014   |
| <b>SK 3978</b>        | <i>P. robustus</i> | Mandible with deciduous molars and developing permanent tooth crowns   | Bromage 1987; Beynon & Dean, 1988; Aiello et al 1991; Conroy & Vannier, 1991b; Cofran, 2014   |
| <b>SK 438</b>         | <i>P. robustus</i> | mandibular fragment with dm2   | Mann 1975; Conroy & Vannier, 1991b; Cofran, 2014  |
| <b>SK 47</b>          | <i>P. robustus</i> | crushed skull including maxilla with partial permanent dentition   | Mann 1975; Bromage 1987; Braga 1998   |
| <b>SK 52</b>          | <i>P. robustus</i> | palate and maxilla with partial permanent dentition  | Mann 1975; Bromage 1987; Braga 1998   |
| <b>SK 55a &amp; b</b> | <i>P. robustus</i> | maxilla and mandible with dm2 and developing permanent teeth   | Beynon & Dean, 1988; Cofran, 2014   |
| <b>SK 6</b>           | <i>P. robustus</i> | left mandibular corpus with permanent molars   | Cofran, 2014  |
| <b>SK 61</b>          | <i>P. robustus</i> | mandible with deciduous teeth, M1 emerged and developing permanent tooth crowns  | Bromage 1987; Beynon & Dean, 1988; Aiello et al 1991; Conroy & Vannier, 1991a, b; Cofran, 2014; Smith, T. et al. 2015;  |
| <b>SK 62</b>          | <i>P. robustus</i> | mandible with deciduous teeth and developing permanent tooth crowns  | Bromage and Dean 1985; Bromage 1987; Beynon & Dean, 1988; Aiello et al 1991; Conroy & Vannier, 1991a, b; Kelley & Schwartz 2012; Cofran, 2014; Le Cabec et al., 2015; Smith, T. et al. 2015 |

|                   |                    |  |  |
|-------------------|--------------------|--|--|
| <b>SK 63</b>      | <i>P. robustus</i> | mandible with deciduous teeth and permanent M1 in occlusion, and developing permanent tooth crowns                 | Bromage and Dean 1985; Bromage 1987; Aiello et al 1991; Dean et al., 1993; Conroy & Vannier, 1991a, b; Smith, 2008; Kelley & Schwartz 2012; Cofran, 2014 |
| <b>SK 64</b>      | <i>P. robustus</i> | Mandible with deciduous molars and developing permanent teeth  | Bromage 1987; Beynon & Dean, 1988; Aiello et al 1991; Conroy & Vannier, 1991b; Cofran, 2014  |
| <b>SK71</b>       | <i>P. robustus</i> | mandibular RI2   | Bromage & Dean, 1985   |
| <b>SK73</b>       | <i>P. robustus</i> | mandibular RI1   | Bromage & Dean, 1985   |
| <b>SK 826</b>     | <i>P. robustus</i> | maxillary fragment with partial permanent dentition  | Bromage 1987   |
| <b>SK 839/852</b> | <i>P. robustus</i> | maxilla and mandible with deciduous teeth and permanent incisor and M1 crowns                                      | Beynon & Dean, 1988  |
| <b>SK 841</b>     | <i>P. robustus</i> | mandible with dm2 and developing M1  | Beynon & Dean, 1988  |
| <b>SK 843</b>     | <i>P. robustus</i> | mandible with developing permanent molars  | Bromage 1987; Beynon & Dean, 1988; Cofran, 2014  |
| <b>SK 852</b>     | <i>P. robustus</i> | mandibular fragment with partial deciduous dentition   | Aiello et al 1991  |
| <b>SKW 5</b>      | <i>P. robustus</i> | partial mandible with M3 erupting  | Cofran, 2014   |
| <b>SKX 162</b>    | <i>P. robustus</i> | maxilla with developing permanent teeth I2-M1  | Beynon & Dean, 1988; Braga 1998  |
| <b>SKX 4446</b>   | <i>P. robustus</i> | partial mandible with M3 unerupted   | Cofran, 2014   |
| <b>EM 2368</b>    | <i>P. robustus</i> | molar crown fragment   | Smith, T. et al. 2015  |
| <b>TM 1517</b>    | <i>P. robustus</i> | Left half calvaria; right mandibular corpus with associated dentition; isolated teeth; some fragmentary postcrania | Mann 1975; Braga 1998; Cazenave et al 2020   |
| <b>TM 1536</b>    | <i>P. robustus</i> | mandible with RLI1 RLI2 RLM1   | Smith, T. et al. 2015  |
| <b>TM 1601a-f</b> | <i>P. robustus</i> | Isolated deciduous and permanent teeth – lower right dm1, dc, P3, C, P4, M1 (not                                   | Bromage, 1987  |



|        |                    |   |                       |
|--------|--------------------|---|-----------------------|
|        |                    | thought to represent the same individual) |                       |
| KB5223 | <i>P. robustus</i> | LLI1, LLI2                                | Le Cabec et al., 2015 |

### Predicting the timing of growth and maturation in *Paranthropus*

As noted, one of the key aims of life history reconstruction in extinct hominins has been to determine the duration of the growth and maturation period, the end of which signals the attainment of adult maturity. Early on, research on the life span in extant mammals determined that longevity, and the pace of development and maturation, were highly correlated with brain size and its metabolic and energetic requirements (Sacher 1975; Sacher and Staffeldt, 1974). Harvey and Clutton-Brock (1985) then demonstrated that adult brain and body size were also highly correlated with a number of developmental life history milestones such as the gestation period, age at weaning, and age at first reproduction. In general, this research explained why primates take longer to grow and mature compared to like-sized non-primate mammals, and also why the largest primates have the longest periods of growth.

Smith (1989, 1991) combined Harvey and Clutton-Brock's life history variables in extant primates with published first permanent molar (M1) emergence ages in a sample of 21 living primate species, and demonstrated that adult brain size was highly correlated with M1 emergence age ( $r = 0.98$ ), and thus could theoretically be used to predict M1 emergence timing in extinct hominin species from estimated brain size. Because the M1 is the first permanent tooth to emerge into the oral cavity, and thus marks a developmental transition from 'infant' to 'juvenile', establishing the age of M1 emergence in extinct species provides a useful milestone in a life history context. Smith (1989) also obtained similarly strong correlations for M1 emergence age and other developmental life history variables, including birth weight, age at weaning, and age at first reproduction. Thus, M1 emergence age was identified as a useful proxy for life history timing and the overall period of growth and development.

When this prediction model is applied to extinct hominins, the resulting M1 emergence ages for *Australopithecus* and *Paranthropus* fall within an 'ape-like' range, and those for early *Homo* fall in an intermediate range between the smaller-brained apes and larger-brained modern humans (Smith & Tompkins, 1995; Smith, 1991). This approach suggests that the evolution of life history timing in hominins was determined largely by increases in brain size.

In contrast, research based on microstructural features of tooth enamel to reconstruct crown formation times and ages at death of immature fossil specimens has demonstrated that in addition to the australopiths (including *Paranthropus*), early *Homo* also followed a life history schedule similar to extant apes (Bromage and Dean, 1985; Beynon and Wood, 1987; Dean et al. 1993; Dean et al. 2001; Lacruz et al. 2005). An extended period of growth first evolved in *Homo ergaster/ erectus*, but this period was still not comparable to that in modern

humans (Dean et al. 2001; Dean and Lucas, 2009). Thus, there are discrepancies between M1 emergence age estimations using the regression approach compared to histological and other methods (Kelley & Schwartz, 2012; Smith, Gannon, & Smith, 1995), and life history timing for some early hominin species cannot be modelled on the basis of extant apes or modern humans (see Smith (2013), Kelley & Schwartz (2012) and Robson & Wood (2008) for discussions of M1 emergence relationships with other life history variables).

Adding to the complexity of this approach, the Plio-Pleistocene hominins were all large bodied and large brained compared to other primates, and predictions from a ‘primate model’ (e.g., Smith, 1989a) about how these extinct species might have varied in details of life history are not straightforward (Kelley & Schwartz, 2012; Smith, Gannon, & Smith, 1995; Smith, 2013). Table 31.2 summarises some of the key life history variables available for extinct hominins and extant apes. If brain and/ or body size variation was the key driver of life history variation, it would be expected that *Gorilla* (the largest of extant apes) would have the latest M1 emergence age, weaning age, etc. In addition, *Pongo*, demonstrating a smaller cranial capacity and female body size, should attain life history events such as weaning and first reproduction at earlier ages. It is now clear that there is considerable variation in these parameters within genera (Galbany et al., 2017; McFarlin et al., 2013; Parker, 1999; T. Smith, 2016; Stoinski et al., 2013; van Noordwijk et al., 2018; Wich, Utami-Atmoko, Mitra Setia, et al., 2004), but even for ranges that overlap such as M1 emergence and weaning ages in *Pan* and *Gorilla*, these life history parameters in *Gorilla* can occur at earlier ages compared to *Pan*, and in *Pongo* occur at later ages (Table 31.2). This variation is thought to reflect trade-offs between growth timing and diet, social behaviour and other factors that impact on reproductive fitness. Thus, while brain size and energetics may be a fundamental pacemaker of an organism’s lifespan – and allow reconstruction of a general life history framework - life history theory proposes that there are trade-offs governed by natural selection to maximise reproductive effort in relation to adult mortality rates, and in relation to available energetic resources (Harvey and Clutton-Brock, 1985; Charnov, 1993; Dirks and Bowman, 2007; Robson and Wood, 2008). Thus, there may be considerable variation (i.e., from a regression prediction) because species evolve different solutions (trade-offs) to maximise reproductive effort and minimise adult mortality. Achieving a better understanding of variation in life history parameters among extant apes will inform reconstructions of life history in *Paranthropus* and other extinct hominins. Some of these issues will be addressed further in the discussion.

<INSERT TABLE 31.2 ABOUT HERE>

Table 31.2. A comparison of life history and related variables for a selection of extinct hominins and extant ape genera. Single values represent the average for the genus, and ranges indicate variation observed in extant field studies, or estimation ranges in fossils, as indicated in the notes below.

| Trait   | <i>Australopithecus</i>                                | <i>Paranthropus</i>                                | <i>Pan</i>   | <i>Gorilla</i>                                    | <i>Pongo</i>                                     |
|---|--|--|--|---|--|
| <b>Female cranial capacity (cm<sup>3</sup>)</b> | 443 ( <i>afarensis</i> )<br>460 ( <i>africanus</i> )   | 484 ( <i>boisei</i> )<br>476 ( <i>robustus</i> )   | 350 ( <i>trogloodytes</i> )<br>326 ( <i>paniscus</i> ) | 456 ( <i>gorilla</i> )<br>480 ( <i>beringei</i> ) | 338 ( <i>pygmaeus</i> )<br>341 ( <i>abelli</i> ) |
| <b>Female body mass (kg)</b>                    | 29 ( <i>afarensis</i> )<br>30 ( <i>africanus</i> )     | 34 ( <i>boisei</i> )<br>32 ( <i>robustus</i> )     | 41.6   | 71.5  | 35.8   |
| <b>M1 emergence age (yrs)</b>                   | 2.95 ( <i>afarensis</i> )<br>3.22 ( <i>africanus</i> ) | 3.00 ( <i>boisei</i> )<br>3.40 ( <i>robustus</i> ) | 4.0 <sup>a</sup><br>2.8- <4.3 <sup>b</sup>             | 3.8   | 4.6  |
| <b>Weaning age (yrs)</b>                        | 3-4  | 2.5-3.5  | 5.0<br>4.3-6.1 <sup>c</sup><br>4.1 <sup>e</sup>        | 3.2<br>3.4-4.7 <sup>d</sup><br>2.8 <sup>e</sup>   | 7.0<br>6.0 <sup>e</sup>                          |
| <b>Age first reproduction (yrs)</b>             | --   | --   | 14.3   | 10.1  | 15.7   |
| <b>Survivorship (yrs)</b>                       | --   | --   | 29.7   | 20.6  | 43.0   |

Notes: Table modified from Kelley & Schwartz 2012, Tables I and II, and other sources as below.

Data for cranial capacity, female body mass, M1 emergence age, age first reproduction, and survivorship in extant apes are from sources in Kelley and Schwartz 2012, Table I:

Cranial capacity: *Pan* and *Homo* (Smith et al. 1995); *Gorilla* (Falk et al., 2000); *Pongo* (Taylor & van Schaik, 2007). Data for cranial capacity in *Australopithecus* and *Paranthropus* species from sources cited in Kelley and Schwartz 2012, Table II: (Conroy et al., 1998; Falk et al., 2000; Holloway, R. L., & Yuan, 2004; Holloway, 1988; Kimbel & Rak, 2010; Suwa et al., 1997).

Female body mass: Smith & Jungers (1997). Female body weights for *Australopithecus* and *Paranthropus* species are from McHenry and Coffing (2000).

M1 emergence age: *Pan troglodytes* – a, skeletal sample of wild chimpanzees (T. M. Smith et al., 2010; Zihlman et al., 2004); b, high-resolution photographic analysis of living wild *Pan troglodytes schweinfurthii* (Machanda et al., 2015); *Gorilla gorilla* and *Pongo pygmaeus* – dental histology of wild shot individuals from museum skeletal collections (Kelley and Schwartz 2010). M1 emergence ages are the average of maxillary and mandibular M1, except in *Gorilla* (mandibular M1 only). M1 emergence age estimates for *Australopithecus* and *Paranthropus* species are predictions from regression analysis from Kelley & Schwartz 2012, Table II.

Mean values for weaning ages for extant apes are from Humphrey (2010) and are similar to those provided by Aiello et al. (1991), Godfrey et al. (2001), and Smith et al. (2017). Ranges are from:

c, Machanda et al. 2015 for weaning age in wild *Pan troglodytes schweinfurthii*;

d, range of population means for weaning age from Stoinski et al. (2013) Table 3 for wild *Gorilla beringei beringei* (3.4y), and captive (3.8y) and wild (4.7y) *Gorilla gorilla gorilla* with an overall range of 1.8 – 6.1 years);

e, compiled averages of weaning age data from Alvarez (2000) for several populations for *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*.

Weaning ages for extinct hominins are broad estimates inferred from Aiello et al., 1991 and represent the age range of specimens either with (*Paranthropus*) or without (*Australopithecus*) heavy deciduous tooth attrition which is an indication for the consumption of solid foods. The key interpretation of that paper is that *Paranthropus* (like *Gorilla* among extant apes) demonstrates evidence for relatively earlier weaning (heavier deciduous tooth attrition) compared to *Australopithecus*. See text for further details.

Age at first reproduction and survivorship data from sources cited in Kelly & Schwartz (2012) Table I: *Gorilla* (Bronikowski et al., 2011; Watts, 1991; Yamagiwa & Kahekwa, 2001); *Pan* (Boesch & Boesch-Achermann, 2000; Hill et al., 2001); *Pongo* (Knott et al., 2009; Wich et al., 2004). Life history data in extant apes represent *Gorilla beringei beringei*, *Pan troglodytes verus* (Tai Forest, Ivory Coast), *Pongo pygmaeus pygmaeus* (Borneo).

### Pattern and timing of dental development in *Paranthropus*

Fortunately, the dental fossil record provides a wealth of information allowing the comparison of the pattern and timing of growth and development among species.

*Paranthropus* fossils demonstrate a dental development pattern that has been described as ‘human-like’ because the permanent I1 is documented at similar (but accelerated) stages of crown or root formation as the M1 throughout the developmental period, as observed in modern human juveniles (Conroy, 1988; Conroy & Vannier, 1991b; Dean, 1985b). However, premolar crown development in *Paranthropus* has already begun at the time of M1 crown completion, unlike either modern human or chimpanzee dental development patterns (Conroy & Vannier, 1991a; Kuykendall, 2003). There is potential evidence in one *P. boisei* specimen for overlap of M1 and M2 crown development (Dean, 2010) similar to *Pan*, but the available fossils are not complete enough to clearly document the pattern of molar (M1-M2-M3) crown formation. Variation in dental development must be affected by a variety of factors during growth, but there is a general level of coordination between the timing and pattern of dental development and facial growth (Conroy & Vannier, 1987; Rodrigo S Lacruz et al., 2019; Lavelle et al., 1977), and between tooth size and morphology with the available space in developing jaws (Boughner, 2011; Conroy & Vannier, 1991b). However, these relationships are not straightforward or fully understood (Boughner & Dean, 2004).

As already noted, the timing of M1 emergence into the oral cavity is a commonly used proxy for the overall pace and timing of life history (Smith, 1989; Smith, 1991). Precise estimates for age at death and M1 emergence age have been estimated from features of enamel microstructure in a small sample of fossil hominins (Beynon & Dean, 1988; Bromage, 1987; Conroy, 1988; Conroy & Kuykendall, 1995; Conroy & Vannier, 1991a, 1991b; Dean, Beynon, Thackeray, & Macho, 1993; Dean, 2006; Kelley & Schwartz, 2012; Lacruz, Rozzi, & Bromage, 2005; Lacruz et al., 2006; Ramirez-Rozzi, 1993; Smith, 1994; Smith et al., 2015). (Kelley & Schwartz, 2012). Table 31.3 summarises the available estimates for age at death and M1 emergence status from studies of dental histology, stage of eruption, and other dental features in fossil hominins. At present, there are no available estimates of M2 and M3 – or other permanent teeth - emergence ages in extinct hominins (Dean, 2010, 2016) but such

information would be extremely useful for improving our understanding of the overall timing and schedule of dental development in extinct hominins.

Table 31.3 includes specimens in a range of extinct hominins that have either not yet emerged or have very recently emerged the M1 tooth; ages provided are age at death estimates from dental histology and other methods. There are no specimens of any species with an estimated age at death of less than 3.0 years that exhibit an emerged M1 tooth, but M1 is emerged in nearly all specimens aged between 3-4 years or older suggesting an estimate for M1 emergence age of about 3.5 years. This is early compared to mean M1 emergence ages among extant apes, which generally range from 3.8-4.6 years (Kelley & Schwartz, 2010, 2012; but Machanda et al., 2015 have reported M1 emergence ages in wild chimpanzees at 2.8-4.3y, see Table 31.2), but it is not yet clear how extinct hominins actually varied in M1 emergence timing. Obtaining accurate ages at M1 emergence in extinct species is challenging as most hominin fossils do not represent individuals who conveniently died just as the M1 had emerged into the oral cavity; various estimations and assumptions are required (Kelley & Schwartz, 2012; Smith et al., 2015b).

Samples of specimens for which more accurate estimates of M1 age are available remain very small. Estimated M1 emergence ages for three *Paranthropus* specimens have been produced by several researchers, and together range from roughly 3.0-3.8 years: SK62 (3.8-3.9y), SK 63 (2.9-3.2y), KNM- ER 1820 (2.7-3.3y) (Bromage & Dean, 1985b; Dean, 1987; Kelley & Schwartz, 2012). For comparison, similar ages for M1 emergence in *Australopithecus* are estimated for Taung (3.3-3.5y), Sts 24 (3.9y) and LH 2 (2.9y). While it is impossible to assess variation adequately from such small samples, M1 emergence ages appear to overlap considerably in *Paranthropus* and *Australopithecus* (Kelley & Schwartz, 2012; Smith et al., 2015b). This is unexpected given previous conclusions that *Paranthropus* attained life history stages earlier than other hominins (Kuykendall, 2003), but may reflect the high correlation between adult body and brain size and the impact of these traits on at least some developmental aspects of life history (Harvey & Clutton-Brock, 1985; B. Smith, 1989).

<INSERT TABLE 31.3. ABOUT HERE>

Table 31.3. A summary of published age at death estimates and M1 emergence status for a sample of early hominin fossil specimens.

| Specimen            | Species              | M1 emergence status           | Age at death estimate (y) | Reference(s)                          | Source of age estimate  |
|---------------------|----------------------|-------------------------------|---------------------------|---------------------------------------|---|
| <b>KNM-KP 31712</b> | <i>Au. anamensis</i> | M1 not emerged                | 2.8                       | Smith, et al., 2015                   | incremental dental development  |
| <b>KNM-KP 34725</b> | <i>Au. anamensis</i> | M1 emerged with occlusal wear | 3.63/4.25                 | Smith, et al., 2015                   | incremental dental development  |
| <b>DIK-1-1</b>      | <i>Au. afarensis</i> | M1 not emerged                | 3                         | Alemseged et al., 2006                | crown and root formation from CT scans                                      |
| <b>LH 2</b>         | <i>Au. afarensis</i> | M1 emerged and in occlusion   | 3.25                      | Bromage & Dean, 1985                  | perikymata counts on mand RI1   |
|                     |                      |                               | ~3.5                      | Beynon and Dean, 1988                 | perikymata counts, crown and root formation (radiographs) & eruption status |
| <b>Sts 2</b>        | <i>Au. africanus</i> | M1 not emerged?               | 2.52                      | Smith, et al., 2015                   | incremental dental development  |
| <b>Sts24</b>        | <i>Au. africanus</i> | M1 emerged                    | 3.3                       | Bromage & Dean, 1985                  | perikymata counts on maxillary RI1  |
|                     |                      |                               | 4.35                      | Smith, et al., 2015                   | incremental dental development  |
| <b>MLD 11/30</b>    | <i>Au. africanus</i> | M1 emerged                    | 3.42                      | Smith, et al., 2015                   | incremental dental development  |
| <b>Taung</b>        | <i>Au. africanus</i> | M1 emerged                    | ~3.5                      | Bromage 1987; Conroy & Vannier 1991a; | Radiographic/ CT assessment of crown and root formation                     |
|                     |                      |                               | 3.73-3.93                 | Lacruz et al., 2005                   | molar crown and root formation  |
| <b>Stw 151</b>      | <i>Au. africanus</i> | M1 emerged                    | 5.2 - 5.3                 | Moggi-Cecchi et al., 1998             | crown and root formation, perikymata counts                                 |
| <b>KNM-ER 1477</b>  | <i>P. boisei</i>     | M1 not emerged                | 2.5 - 3.0                 | Dean, 1987                            | perikymata counts, crown and root formation (radiographs) & eruption status |

|                    |                    |                 |             |                     |   |
|--------------------|--------------------|-----------------|-------------|---------------------|---|
| <b>KNM-ER 812</b>  | <i>P. boisei</i>   | M1 not emerged  | 2.5 - 3.0   | Dean, 1987          | perikymata counts, crown and root formation (radiographs) & eruption status |
| <b>KNM-ER 1820</b> | <i>P. boisei</i>   | M1 emerged      | 2.5 -3.1    | Dean, 1987          | perikymata counts, crown and root formation (radiographs) & eruption status |
| <b>OH 30</b>       | <i>P. boisei</i>   | M1 not emerged  | 2.7 - 3.2   | Dean 1987           | perikymata counts, crown and root formation (radiographs) & eruption status |
| <b>DNH 47</b>      | <i>P. robustus</i> | M1 not emerged? | 0.67 - 0.77 | Smith, et al., 2015 | incremental dental development  |
| <b>TM 1536</b>     | <i>P. robustus</i> |                 | 1.63 - 2.02 | Smith, et al., 2015 | incremental dental development  |
| <b>DNH 44</b>      | <i>P. robustus</i> | M1 not emerged  | 1.7         | Smith, et al., 2015 | incremental dental development  |
| <b>DNH 84</b>      | <i>P. robustus</i> | M1 not emerged? | 2.24        | Smith, et al., 2015 | incremental dental development  |
| <b>SK 63</b>       | <i>P. robustus</i> | M1 emerged      | 3.15        | Bromage & Dean 1985 | perikymata counts on mandibular RI1   |
|                    |                    |                 | 3.18-4.23   | Dean et al., 1993   | incremental dental development, CT assessment of crown and root formation   |
| <b>SK 62</b>       | <i>P. robustus</i> | M1 not emerged  | 3.35 - 3.48 | Bromage & Dean 1985 | perikymata counts on mandibular RI1 & LI2                                   |
|                    |                    |                 | 3.12        | Smith, et al., 2015 | incremental dental development  |
| <b>DNH107</b>      | <i>P. robustus</i> | M1 emerged      | 4.82        | Smith, et al., 2015 | incremental dental development  |
| <b>DNH 108</b>     | <i>P. robustus</i> | M1 emerged      | 5.35/ 5.53  | Smith, et al., 2015 | incremental dental development  |

Notes: The two age at death estimates for KNM-KP 34725, DNH 108 were calculated using different periodicity values (in T. Smith et al 2015). See (T. Smith, 2008, Table 3) and (T. Smith et al., 2015, Table 3) for age at death summaries of additional fossil specimens from incremental dental development.

Another aspect of dental development that provides some information about variation in the scheduling of growth and development is the timing of the crown formation period. It might seem logical to predict that the larger and more thick-enamelled teeth of early hominins would require a longer period in which to secrete and mineralize enamel during development. However, available estimates of crown formation times (CFTs) in extinct hominins and extant apes and humans (Table 31.4 and Figure 31.1) demonstrate otherwise. The CFTs for most teeth in extinct species are shorter compared to those of extant apes and humans, especially for the anterior teeth – but the I1 in *Au. africanus* compared to *Gorilla*, and all M1s compared to *Pan* are exceptions. In most taxa other than *Paranthropus* the CFTs of anterior teeth are longer than the CFTs of postcanine teeth. For *Pan* and perhaps other apes (data are limited), anterior tooth crowns take longer to form perhaps due to larger crown size especially for canines. In *Au. africanus*, Le Cabec et al. (2015) calculated the CFT for the unerupted canine crown at 5 years, considerably longer than the average reported by Smith et al. (2015) which may indicate sex dimorphism or other sources of developmental variation. In contrast, CFTs in the larger, thick-enamelled *Paranthropus* molars are shorter compared to all other species except *Au. afarensis* and *Pan* M1s, but molar CFTs for extinct hominins are shorter than those in modern humans and generally more similar to those in *Pan* (Dean, 2010). Human molars – the smallest in size – demonstrate the longest CFTs among taxa represented. Size differences alone do not explain the observed variation in CFTs between tooth types or species.

[INSERT TABLE 31.4. Crown formation times about here]

Table 31.4. A comparison of estimated average permanent crown formation times (CFTs) in *Paranthropus*, *Australopithecus*, early *Homo*, extant apes and modern humans.

| Tooth type | <i>Au. afarensis</i> | <i>Au. africanus</i> | <i>P. boisei</i> | <i>P. robustus</i> | <i>Pan</i>    | <i>Gorilla</i> | <i>Pongo</i>  | <i>H. sapiens</i> |
|------------|----------------------|----------------------|------------------|--------------------|---------------|----------------|---------------|-------------------|
| I1         | 3.3                  | 3.80                 | 2.20             | 2.44               | 4.67          | 3.13           |               | 3.59              |
| I2         |                      | 3.23                 |                  |                    | 4.42          | 3.81           |               | 3.49              |
| C          | 3.60                 | 2.78/ 5.0            | 2.40             | 3.25               | 6.81/<br>5.85 | 8.54/<br>5.64  | 8.73/<br>5.47 | 4.64              |
| P3         | 3.00                 | 2.81                 | 2.54             | 2.11               | 3.53          |                |               | 3.37              |
| P4         |                      | 2.89                 |                  |                    | 2.25          |                |               |                   |
| M1         | 2.20                 | 2.41                 | 2.63             | 2.17               | 2.05          | 2.66           | 3.01          | 2.87              |
| M2(M3)     | (2.35)               | 2.75                 | --               | 2.44               | 2.76          | 3.02           | 3.44          | 2.94              |

Notes: Sample sizes for the different teeth and species are highly variable, and difficult to determine since these data are compiled across different studies using different methods, samples, cusps, etc. For a given tooth type, the *H. sapiens* samples include at least 30 and, in some cases, >100 teeth (Table 1, Reid & Dean (2006), while CFTs for fossil hominin species are generally based on small samples of 2-3 or single teeth. Ramirez-Rozzi (1995) provided CFTs for a sample of 21 premolars and 45 molars of *P. boisei* but not all were identified to specific tooth types, and the analysis produced



average CFTs only for 'premolars' and 'molars'. For any species, CFTs for different tooth types usually derive from different individuals (see references cited below).

Average values for *Au. africanus*, *P. robustus*, *Pan*, *Gorilla* and modern humans are derived from Table 2 in T. Smith et al. (2015). The estimated average CFTs above were calculated by converting the average crown formation times (in days) from Table 2 in T. Smith et al., (2015) into years and calculating the mean CFTs for all cusps per tooth type (maxillary and mandibular) to maximise available data. Data for *Pongo* molars are from T. Smith (2016) Table 10 and were calculated in the same manner. Data for extant ape canine crown formation times are from Schwartz & Dean (2001), Table 4, and represent male/female values. For *Au. africanus* canines, Le Cabec et al. (2015) reported a CFT of 5 years for the MLD2 individual. For *H. sapiens*, the mean CFT for the two populations (Eur and SA from Reid and Dean (2006)) were calculated.

CFT estimates for *Au. afarensis* I1, C, P3 are from Kuykendall (2003), Table 8.1 and are derived from Bromage & Dean (1985) and Beynon & Dean (1988) (Table 2). CFTs for *Au. afarensis* molars are from Lacruz & Ramirez-Rozzi (2010), Table 2. The CFT for *Au. afarensis* M3 is the midpoint of the range 2.3-2.4 years from that source.

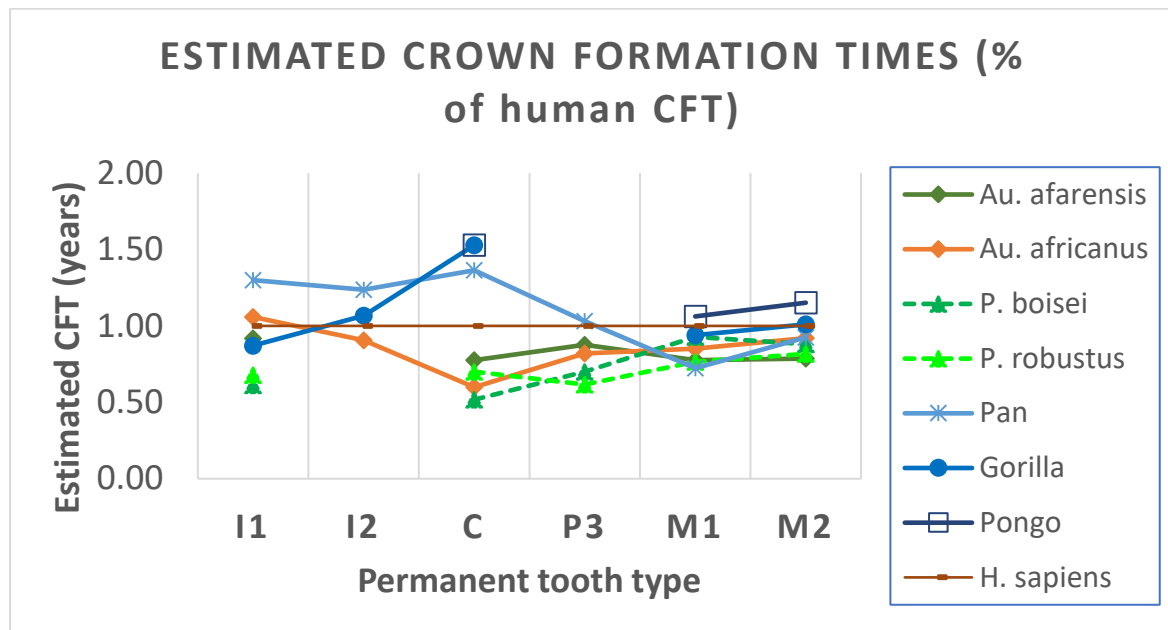
Data for *P. boisei* are derived from Beynon & Wood (1987), Dean (1987a), Beynon & Dean (1987), and Ramirez-Rozzi (1993, 1995). These sources do not all provide CFTs for all individual tooth types, so the M1 CFT presented is an average CFT of the published ranges (midpoint, mean) for different combinations of M1, M2 and M3 teeth - 2.12-2.59 (2.35) for M1s & M3s in Beynon and Wood (1987), 2.67-3.43 (2.99) in Ramirez-Rozzi (1993) for M3s, and a mean of 2.56 (1.8-3.4) for a sample of M1-M3s in Ramirez-Rozzi (1995). Ramirez-Rozzi (1995) provided a mean CFT for premolars of 2.54 years, with a range of 1.8-3.1 years, listed above for the P3.

It is acknowledged that crown formation is more complex than such average estimates per tooth indicate, but these estimates represent the range of published results using different techniques and samples.

In terms of the percentage of human CFTs (Figure 31.1), the CFTs for incisors, canines and premolars in *Paranthropus* are extremely short compared to other taxa. Molar CFTs among Plio-Pleistocene hominin species are generally more similar and shorter than extant apes and humans (except *Pan*) but those in *Paranthropus* are in the lower range overall. It is also noted that the CFTs in postcanine teeth for *P. robustus* tend to be shorter than other species, including *P. boisei*. Data are not complete for all tooth types, and sample sizes are variable and small, but CFTs among all tooth types in *Paranthropus* demonstrate a different pattern from any other taxon.

<INSERT Figure 31.1 about here – plot of CFTs (%) in hominin species >

Figure 31.1. Crown formation times expressed as a percentage of human CFTs for extinct hominins and extant apes. Data not available for all tooth types in all species. Data sources as listed in Table 3.



Growing larger (or smaller) teeth in shorter (or longer) periods is accomplished by variation in daily secretion rates or extension rates of enamel, which is manifest in the orientation of Striae of Retzius in enamel and the distribution of perikymata on the tooth surface. (Beynon & Dean, 1988; Dean, 2000; Dean & Reid, 2001; Ramirez-Rozzi, 1993; Schwartz & Dean, 2000). While it is debated whether CFTs have relevance to predicting life history schedules (Kelley & Smith, 2003; Macho, 2001) they must reflect variation in species' strategies to allocate developmental time and energy to production and maintenance of adaptive structures. While brain and body size remain the strongest correlates of ontogenetic variation (Harvey and Clutton-Brock, 1985; Smith, 1989), strong correlations have been reported between variables reflecting precocity in dental eruption (Godfrey et al. 2001) and factors of enamel development (Hogg and Walker 2011) with ecological variables relating to independent foraging, maternal investment and risk aversion in primates.

Thus, while different early hominins may have developed and erupted their teeth within a general developmental framework that was similar to extant apes (i.e., shorter than in modern humans), the timing and pattern of different components of dental development – formation periods for individual tooth crowns and roots, tooth emergence ages, etc – all appear to vary among species and it can be predicted that such variation is at some level a reflection of differences in ecology. The key life history question regarding the observed shorter CFTs in *Paranthropus* is why a primate that is similar to other extinct species in cranial capacity, body size, M1 emergence age and probably its overall growth and maturation schedule needed to develop tooth crowns in a shorter period of time. The observation of shorter CFTs in both small-crowned anterior teeth and very large, thick-enamelled premolars and (to a lesser degree) molars is a unique pattern in *Paranthropus* compared to the other species (Table 31.4, Figure 31.1).

## Other aspects of growth and development in *Paranthropus*

Growth and maturation in any species involves a complex array of events and processes culminating in the attainment of adult size, form and function. Such events must be highly coordinated, and phylogeny, genetic regulation, adaptation and natural selection must be involved in different ways. However, in a palaeoanthropological context the detailed understanding of the complete growth and development period for any extinct hominin species is limited by the fragmentary condition of fossils, lack of immature specimens comprising an age series, uncertainty of phylogenetic relationships and lack of complete growth data in a wide comparative sample of extant apes and other primates. Even with these limitations, there is a compelling body of research about cranial and mandibular growth, weaning and sex dimorphism in *Paranthropus* compared to other taxa.

### *Cranial and somatic growth and maturation*

Comparisons of growth in cranial bones in extinct hominins, extant apes and humans have been interpreted in the context of facial prognathism, permanent tooth size and development, masticatory biomechanics, and other factors. SEM image analysis of *Paranthropus* (primarily *robustus*) cranial fossils demonstrate that the anterior surfaces and anterolateral surfaces of the maxilla and mandible are resorptive, indicating an inferiorly-directed growth vector (Bromage, 1989; Lacruz et al., 2019). Osteological observation of *Paranthropus* cranial fossils demonstrates that fusion of the incisive suture is completed relatively early (Braga, 1998; Maurelle & Braga, 2002). Both of these patterns of facial bone growth are shared with humans and are thought to be associated with the reduced facial prognathism of both taxa. In contrast, more prognathic species of *Australopithecus* and *Pan* are characterized by depositional anterior surfaces of facial bones indicating an anteriorly-directed growth vector (Bromage, 1989) and relatively late fusion of the incisive suture (Braga, 1998). However, these characterisations of facial growth and remodelling in prognathic and non-prognathic species are likely to be oversimplified; *Paranthropus* demonstrates reduced prognathism only relative to *Australopithecus*. *Paranthropus* facial and mandibular remodelling differs from other species in relation to the effect of the extreme degree of posterior facial height on other facial regions such as the orbits and the pterygoid region, and in the posterior mandibular corpus due to large molar tooth size (Bromage, 1989). In a re-assessment of facial remodelling employing a larger comparative sample of *Pan*, *Homo sapiens* and fossil hominins, McCollum (2008) determined that the nasoalveolar clivus in *Pan* (prognathic) also exhibits resorptive fields at some ontogenetic stages – similar to *P. robustus* (orthognathic).

McCollum (1997, 1999; McCollum & Ward, 1997) analysed variation in the arrangement of the bones of the subnasal alveolar region, and in relation to thickness of the hard palate in extant apes and extinct early hominins. The distinctive morphology of these structures in *Paranthropus* includes the extension of the vomer anteriorly onto the nasal surface of the premaxilla, an anteriorly thickened hard palate, and an extreme degree of maxillary rotation associated with an unusually tall mandibular ramus (Mccollum, 2008). The ontogenetic pattern that produces a high degree of maxillary rotation, and the thickened anterior hard palate in *Paranthropus* is similar in some aspects to that of *Pan*, but it is uniquely modified in *Paranthropus* due to its orthognathic facial profile, relatively tall posterior maxilla (and by

extension the mandibular ramus), small anterior dentition, and extremely large postcanine dentition. These differences are associated biomechanically with the extreme expression of masticatory structures of the *Paranthropus* cranium and mandible.

Cofran (2014) analysed 28 linear measurements from a series of immature *Paranthropus robustus* and modern human mandibles in order to assess differences in the proportional increase in size between molar tooth eruption stages. The proportional size increases between older and younger samples of *Paranthropus* indicate that growth rates were generally greater than those in *Homo*, and that major differences in mandibular growth coincide with emergence of the permanent M1, and then the M2. This appears to be congruent with evidence from dental hard tissues (Beynon & Dean, 1988; Dean, Beynon, Thackeray, & Macho, 1993; Lacruz et al., 2006) in that short CFTs would produce large tooth crowns at earlier ages and mandibular growth would be required to accommodate those structures. Thus, differences in postnatal growth and the timing of growth spurts result in the observed differences in mandibular shape and size between *Paranthropus* and *Homo*. Similar data for other ape and hominin species is needed to further illuminate these observations.

A strong correlation between M1 emergence age and other life history variables, including weaning age, has been reported (Smith, 1992), and the timing of M1 emergence and weaning has been suggested to be roughly equivalent. More recent observations from field studies of wild primate populations (Bădescu et al., 2017; Eckardt et al., 2016; Lee, 1996; Smith, Austin, Hinde, Vogel, & Arora, 2017; Smith, Machanda, et al., 2013) indicate that this relationship is not so straightforward. The weaning age for a species is an informative life history parameter, as it marks the transition to solid foods, increased independence of offspring, and is at least a rough indication of a species' reproductive rate (Aiello et al., 1991; Stoinski et al., 2013). However, both the event and process of weaning can vary among closely related species due to a complex interplay between maternal energetics and social and ecological factors affecting both mother and infant (Aiello, Montgomery, & Dean, 1991; Humphrey, 2010; Kelley & Schwartz, 2010; Lee, 1996; Smith et al., 2013).

In an early study to assess weaning age in extinct hominins, Aiello et al. (1991) compared patterns of deciduous tooth wear in extant apes and extinct hominins, noting that *Gorilla*, *Paranthropus*, and *Au. africanus* demonstrate higher degrees of deciduous tooth wear compared to other species (more recently, a specimen from Drimolen demonstrating similar tooth wear has also been reported by Moggi-Cecchi et al. (2010; also Dean, 2010)). The presence of deciduous tooth wear indicates that solid foods had been introduced, and thus the weaning process was initiated even if not complete. In at least some of the specimens, wear on deciduous teeth is present before the M1 is fully erupted but similar estimated ages at death were attributed to specimens both with and without the M1 emerged (also see Table 31.3). Estimated ages at death were between 2.5-3.5 years for *Paranthropus* (demonstrating high levels of deciduous tooth wear) versus 3-4 years for *Au. afarensis* (demonstrating unworn deciduous teeth). These differences in deciduous tooth wear and age at death estimates between *Paranthropus* and other extinct hominin taxa may indicate differences in weaning schedules, suggesting that weaning age for *Paranthropus* is comparable to *Gorilla*, but younger than *Pan* or *Pongo* (Table 31.2). However studies of weaning across primate species suggest that the timing and process of weaning and the introduction of solid foods –

and presumably the degree of deciduous tooth wear - varies widely among both different primate species, and among different populations of the same species (Lee, 2012; Machanda et al., 2015; C. Smith et al., 2010; T. Smith et al., 2017; Stoinski et al., 2013). In wild chimpanzees, the introduction of solid foods can start in the first few months of life (Bădescu et al., 2017; T. Smith et al., 2013), well before M1 gingival emergence. Further research is needed to more fully understand the factors influencing variation in the weaning process in relation to observable aspects of the fossil record such as deciduous tooth wear and M1 emergence timing and thus inform palaeobiological inferences.

Sex dimorphism has been observed in most species of early hominin, including those of *Paranthropus* (McHenry, 1994; Plavcan & Van Schaik, 1997), and has implications for interpreting growth and socioecological behaviour. Based on seriation of dental wear patterns and a series of size-related measurements in a sample of *P. robustus* crania, Lockwood et al. (2007) determined that cranial growth in males appears to have extended beyond the completion of dental development, but in females was completed at roughly the same time. This pattern of bimaturism appears generally similar to that observed in *Gorilla* and *Pongo* but differs from the growth pattern of *Pan* (Leigh & Shea, 1996; Leutenegger & Masterson, 1989; Utami, 2002). While it is recognised that sex dimorphism and bimaturism are important aspects of variation in growth and life history, until recently these parameters have been largely absent from evolutionary models about hominin life history and remain to be adequately incorporated.

### Toward a primate perspective: A discussion of *Paranthropus* life history

This review aimed to answer the question, ‘In life history terms, what kind of primate was *Paranthropus*’? An overview of key features of *Paranthropus* ontogeny and life history is presented in Table 31.5. The available fossils suggest that *Paranthropus* was a large-bodied, relatively large brained primate exhibiting a strong degree of sex dimorphism. Because body size is highly correlated with the timing of life history as reflected in the ‘fast-slow continuum’ concept, and also reflects a phylogenetic grade-shift in hominoids, *Paranthropus* was likely to have been relatively late-maturing and long-lived among primates, in line with known life history schedules for similar-sized extant apes and those inferred for *Australopithecus* and extinct hominoids (Kelley, 1997; Kelley & Smith, 2003). However, it does not appear likely that *Paranthropus* grew up like other early hominins, or like any extant ape.

< INSERT TABLE 31.5 ABOUT HERE >

Table 31.5. Overview of *Paranthropus* growth and life history: In life history terms, what kind of primate was *Paranthropus*?

| Overview of <i>Paranthropus</i> growth and life history   |   |   |   |
|---|---|---|---|
| Morphology  | Ontogeny  | Demography  | Diet  |
| <ul style="list-style-type: none"> <li>Female body mass 32-34 kg, perhaps slightly larger than other extinct hominins but smaller than extant apes</li> <li>Adult brain size 476-484 cc, at the upper end of the range including <i>Australopithecus</i> and extant apes</li> <li>Large thick-enamelled dentition; heavy masticatory muscle attachments compared to other hominins, but some traits (thick enamel, sagittal crest) also occur in other species</li> </ul> | <ul style="list-style-type: none"> <li>M1 emergence age 3.0-3.4 years, roughly comparable to other extinct hominin species but younger than extant apes</li> <li>CFTs relatively short for all teeth, but especially incisors, canine and premolars</li> <li>Anterior tooth CFTs slightly shorter in <i>P. boisei</i>; molar CFTs slightly shorter in <i>P. robustus</i></li> <li>Weaning age estimated to be in the range 2.5-3.5 years; younger than estimates for <i>Australopithecus</i> and recorded weaning ages for extant apes. Deciduous tooth wear indicates that supplementary foods were consumed at a very young age</li> <li>High sex dimorphism in body size probably resulted in bimaturism with</li> </ul> | <ul style="list-style-type: none"> <li>Apparently high mortality of infants and very young individuals based on known fossil assemblages</li> <li>Probably high predator risk for subadults and young adult males</li> <li>On the basis of strong body size sex dimorphism, social groups may have involved high inter-male aggression and competition, and thus young males may have lived in solitary or multi-male groups. Dominant males may have controlled mating access to multiple females. The lack of strong canine dimorphism may counter this reconstruction</li> </ul> | <ul style="list-style-type: none"> <li>Largely plant-based, including low-quality fibrous and/or hard-object food items</li> <li>Probably includes consumption of invertebrates such as termites, at least at South African sites such as Swartkrans</li> <li>C3 isotope profile for <i>P. boisei</i>; C4 isotope profile for <i>P. robustus</i></li> <li>Diet quality, seasonal availability, distribution and related factors may constitute ecological risks that would have varied at different localities across the geographic</li> </ul> |

|  |   |  |                    |
|--|---|--|--------------------|
|  | males having an extended growth phase beyond dental and sexual maturity; the concurrent lack of sex dimorphism in canines is unique |  | range of the genus |
|--|---|--|--------------------|

The growth and development of the unique *Paranthropus* facial form appears to be a mosaic of phylogenetically shared patterns and processes among hominoids, and genus- or perhaps species-level adaptations to produce the biomechanically efficient structures required to process hard or tough food items. The processes that facilitate dental development and other aspects of growth and development, such as enamel formation, tooth eruption, and bone remodelling are essentially the same among species (Dean, 1989; Schwartz & Dean, 2000), but variation in timing (initiation and completion, duration) and pattern (sequence and relative development) of such ontogenetic packages among closely related species may be informative about life history strategies and broader aspects of adaptation (Beynon et al., 1991; Beynon & Dean, 1988; Kelley, 1997; Kelley & Schwartz, 2010). Thus, the *Paranthropus* life history schedule exhibits phylogenetically shared features such as the timing of M1 emergence at a similar age to other extinct hominins and extant apes of similar body size, but also an earlier weaning age and shorter CFTs. This combination is puzzling – why develop tooth crowns early when emergence is not also accelerated? It may indicate a life history trade-off regarding food processing requirements and the introduction of solid foods during weaning, but any suggested sources of selection would be speculative. It should be noted that estimated emergence age for extinct hominins are only available for the M1, and M1 CFTs show less interspecific variation compared to CFTs for other tooth types (Table 31.4, Figure 31.1) perhaps reflecting the significance attributed to M1 emergence timing as a stable developmental marker. Future research to determine emergence ages of all permanent tooth types would be informative in understanding this pattern.

This mosaicism is evident in similarities in the pattern of cranial bone remodelling between the more prognathic (*Australopithecus*, *Pan*) and the less prognathic (*Paranthropus*, *Homo*) taxa, but not all aspects of ontogenetic variation adhere to this pattern. In reality *Paranthropus* can only be regarded as an orthognathic taxon in comparison to *Australopithecus* and extant apes, and the facial profile varies considerably among individual specimens. *Paranthropus* differs from *Homo* in premolar and molar dental development, CFTs for all teeth, developmental features of tooth microstructure, and the pattern and relative rates of mandibular growth. Other aspects of *Paranthropus* facial ontogeny such as the high degree of maxillary rotation are similar to *Pan*. In addition, available data suggest that *P. robustus* and *P. boisei* vary in the pattern and timing of developmental events such as

M1 emergence ages and crown formation times (Tables 31.3 and 31.4). In a comparative context, this is not surprising: observed differences in other aspects of life history between mountain and western lowland gorillas (Breuer et al., 2009; Stoinski et al., 2013) and between Sumatran and Bornean orangutans (Wich et al., 2004) are explained as responses to differences in environmental risk and variation in diet quality and availability between these closely-related species.

The evidence for early weaning age is another indication that *Paranthropus* grew up in a high-risk or marginal environment (Aiello et al., 1991; Dean, 2010), and early weaning may represent a life history trade-off relating to selection for immatures to attain independence earlier. However, weaning is recognised as a variable process (Humphrey, 2010; Lee, 1996b) involving a number of events that may differ in timing and duration among species – in apes the introduction of solid foods can occur at very young ages well before M1 emergence, but the ultimate cessation of suckling may take years (Smith, et al., 2017; Smith, et al., 2013). What is known is that *Pan*, *Gorilla* and *Pongo* all start and complete the weaning process on different schedules, probably in relation to differences in diet quality, social structure and maternal care (Eckardt et al., 2016; Lee, 1996). Differences in weaning age have been documented between mountain and western lowland gorillas (Stoinski et al., 2013) and are thought to be a consequence of energetic (dietary) and other risk factors including infanticide.

It is necessary to find some compatibility between evidence for weaning available from a variety of methods involving wear on deciduous fossil hominin teeth (Aiello et al., 1991), behavioural observation of extant primates in both captive and wild conditions (Smith, 2013; Smith et al., 2017; Smith, Machanda, et al., 2013; Stoinski et al., 2013), and chemical analysis of tooth enamel of extant or fossil species (Austin et al., 2013; Humphrey, 2014; Humphrey et al., 2008; Tacail et al., 2017). In particular, a recent method combining elemental mapping of barium with the histological analysis of dental development provides a wealth of detail about nursing behaviour and the weaning process in primates (Austin et al., 2013; Smith et al., 2017) that can be contextualised with available observations from wild and/or captive populations. This method has recently been applied to two *Au. africanus* fossil specimens (Joannes-Boyau et al., 2019) and indicates a period of predominant milk consumption peaking at about one year, followed by a cyclical repetitive barium signal ending at 4-5 years of age. This estimate for weaning age in *Au. africanus* is about a year later than that in Table 31.2 based on deciduous tooth attrition, and the weaning process indicated is similar to the cyclical weaning behaviour observed in orangutans (Smith et al., 2017) and other primates adapted to seasonally available diet resources. Clearly, it is important to apply this method to a larger sample of extant primates with diverse weaning strategies, and to other extinct hominin taxa, including *Paranthropus*, and to re-evaluate interpretations about weaning age from degree of deciduous tooth wear in fossils.

In addition, it is worth assessing which aspects of the weaning process are more meaningful for life history comparison and interpretation (Borries et al., 2014; T. Smith et al., 2013) – the introduction of solid foods, M1 emergence or the completion of the weaning process some years later, or the overall duration and/ or cyclicity of the weaning process? For assessments of weaning age in extinct species, how can estimates be improved so that more applicable assessments of data from extant primate populations can be made? Given both the scarcity of



specimens and the differences in the nature of ‘weaning data’ from fossils it is unlikely that current assessments of weaning age in extinct hominins actually correspond with those from wild studies of living primates.

The high degree of sex dimorphism demonstrated among *Paranthropus* specimens also has implications for life history reconstruction. On the basis that the inferred degree of sex dimorphism is more similar to that in *Gorilla* or *Pongo* than to *Pan* or modern *Homo*, Lockwood et al. (2007) inferred that *P. robustus* can be characterised by harem-style social groups, single dominant males, and groups (or isolated individuals) of non-dominant males. Non-dominant isolated males would have been subject to high levels of predation from large carnivores (see also Grine et al 2012). In contrast, Kaszycka (2016) argued that a multi-male multi-female social group is more likely in *Paranthropus* after comparing ecological and social factors among extant primates. In the context of differences in social organisation among apes, Stoinski et al. (2013) discussed the role that social cohesion, gregariousness, and infanticide risk might have on life history timing, but the available data remain inconclusive. One equivocal factor in such reconstructions is that while *Paranthropus* may have been strongly sexually dimorphic in body size, the canine tooth was not dimorphic and exhibited a reduced crown size in both males and females. This is a unique combination among primates and its relevance to understanding life history and sociobiology of the genus is unknown. Further research to elucidate the range of life history solutions observed among extant primates in terms of both the possible impacts on variation in male and female life histories, and the different aspects of socioecological risk in relation to sex dimorphism would be of great interest.

Both this review and previous researchers (Dean, 2010; Kelley & Schwartz, 2012; Lockwood et al., 2007) have noted that different aspects of *Paranthropus* palaeobiology, including aspects of dental development, sex dimorphism, and diet variation, demonstrate similarity with *Gorilla* and possibly *Pongo* rather than *Pan*. Historically, *Pan (troglodytes)* is most commonly referenced as the ‘ape’ species on which early hominin life history reconstructions rely, but the current understanding of variation in a variety of factors relevant to life history among extant apes suggests that *Gorilla* and *Pongo* would be more relevant extant taxa on which to model *Paranthropus* life history. Comparisons involving *Gorilla* and *Pongo* are relevant in improving our understanding of life history variation in relation to diet, sex dimorphism and bimaturism, and possibly different aspects of social behaviour. Aside from apes, relevant variation in diet, social structure and other factors are observed among species of *Papio* (Kaszycka, 2016; Swedell & Leigh, 2006) and also require further consideration.

As noted in Table 31.1 the *Paranthropus* immature fossil assemblage includes a high proportion of very young individuals, particularly for the larger sample of South African *P. robustus* immature specimens at Swartkrans and Drimolen. The *P. robustus* age-at-death distribution has been discussed by McKinley (1971), Bromage (1990), Bromage and Dean (1985), Mann (1975), and Tobias (1999) to consider various causes of high infant mortality. While it is generally accepted that both *Au. africanus* and *P. robustus* fossil assemblages from South African cave sites are a result of large carnivore activity, most probably leopards (Brain, 1981; Frederick E. Grine, Jacobs, et al., 2012; Pickering et al., 2004), the degree and nature of carnivore involvement probably varied among sites (Pickering et al., 2004). The age-at-death distribution for Drimolen differs from that at Swartkrans and is more similar to

the natural population structure of wild apes in the absence of predation, demonstrating a low proportion of young adult specimens (Riga et al., 2019). Even if preservation factors have affected the assemblages for other species, the relatively abundant infant and juvenile *P. robustus* profile is indicative of a high immature mortality rate (Bromage, 1987; McKinley, 1971; Tobias, 1999), suggesting a high risk from predation and other factors. In a life history context, early maturation is expected when the age-at-death profile includes a higher proportion of young adults to immatures – i.e., when reproductive aged individuals are at higher risk from predation or other factors compared to immatures (Isbell et al., 2009). Further comparison of complete mortality profiles from different taxonomic assemblages, and taking into account possible taphonomic factors, will help to clarify the significance of the observed high proportion of young *Paranthropus* fossils, and that of variation in age-at-death distributions from different sites.

One key factor underlying variation in different aspects of life history is diet quality, referring to the digestibility and nutrient content of food sources (Aiello & Wheeler, 1995; Fish & Lockwood, 2003). Simplistically, diet quality is lowest in predominantly folivorous species and improves for species consuming higher proportions of fruits and animal protein. In reality, the varying components of diet in species classified as ‘folivores’, ‘frugivores’, etc make assessment of diet quality more complicated. Diet quality has been shown to have an impact on a range of morphological, behavioural and ecological factors including gut morphology, dentition, brain size, daily activity patterns, and energy budgets (Aiello & Wheeler, 1995; Chivers & Hladik, 1980; Clutton-Brock & Harvey, 1980; Fish & Lockwood, 2003; Leonard & Robertson, 1997). Thus, its relevance to understanding life history variation is wide-ranging.

A number of studies have reported evidence for early maturation in species consuming a low-quality diet – folivory vs frugivory in primates (Godfrey et al., 2001; Leigh, 1994; Parker, 1999); grazing vs browsing in bovids (Macho & Williamson, 2002) – compared to closely-related species of similar body size. The general conclusion is that low-quality but abundant diet resources such as leaves allow rapid maturation and thus help to maximise reproductive rate (Janson & van Schaik, 1993). However, not all studies confirm this pattern. In extant indriids and related subfossil lemurs, Godfrey et al. (Godfrey et al., 2013; Godfrey et al., 2004, 2006; Schwartz et al., 2002) presented evidence that both were dentally precocious but exhibited slower somatic growth compared to frugivorous species, concluding that there was not a ‘one size fits all’ life history relationship with regard to diet. Borries. et al. (2011) found a difference in gestation length, but not in age at first birth or interbirth interval in an analysis of Asian colobines and Asian macaques; life history variables relating to dental and somatic ontogeny were not included in their analysis. While the reasons for these unexpected similarities between folivores and frugivores were not clear, the authors suggested that feeding adaptations may not be the only constraints affecting these life history variables, and energetic requirements at different developmental periods may also be relevant. They also emphasised the rigorous process of data cleaning and careful selection of sources to improve data quality over previous studies. This underlines a real challenge in comparing and assessing results from life history studies, especially involving extant and extinct species. Taken together, different studies in this area might include different variables describing aspects of life history, compile data on a narrower or wider taxonomic range, or address data

quality issues differently. The impact of such methodological differences on interpreting conflicting results is not yet clear.

Another difficulty in applying such research is with the characterisation of ‘diet’ in either extant or extinct species. A variety of methods to reconstruct diets of extinct hominins have been applied, ranging from biomechanical assessment of dental and masticatory morphology (Grine et al., 2010; Smith et al., 2015; Strait et al., 2012; Wood & Strait, 2004), tooth wear (Ungar et al., 2008, 2011), stable isotopes (Cerling et al., 2011; Godfrey, Crowley, & Dumont, 2011; Lee-Thorp et al., 2010; Sponheimer et al., 2013, 2005), enamel microstructure (Macho & Shimizu, 2009), enamel chipping (Constantino et al., 2010; Lucas et al., 2008), and various ecological approaches (de Ruiter et al., 2008; Macho, 2014b, 2015). As might be expected with so many diverse sources of information, the debate continues, but the very general consensus is that *Paranthropus* diets differed from other early hominin species, consisted of either hard or tough food items, and probably derived from a marginal environment. As already noted, dietary differences are indicated by the stable isotope profiles for *P. boisei* and *P. robustus*, and there is evidence that at least *P. robustus* consumed termites based on microwear analysis of bone tools at Swartkrans (Backwell & D’errico, 2001; D’errico et al., 2001). None of these characterisations indicate clearly how to describe the *Paranthropus* diet using terms generally applied to extant species such as ‘folivore’, ‘frugivore’, and ‘omnivore’ even if it was considered to be largely herbivorous. What might a life history perspective add to this discussion?

*Ecological risk and trade-offs.* The Ecological Risk Hypothesis (Janson & van Schaik, 1993:57) describes the juvenile period in primates as ‘one of great ecological risk’, primarily from factors relating to competition for food resources (risk of starvation), or from predation. If resources are abundant, and competition low, individuals should grow and mature quickly in the absence of predation risk in order to initiate reproduction as early as possible. However, in order to survive when resources are patchy or dispersed and competition is high, it is effective for growth rate to slow to reduce metabolic costs so that the risk of starvation per unit time is decreased. Such limits on resources, and selection pressures such as predation result in complex networks of options for life history strategy, or trade-offs (Ross, 1998; Stearns, 1989). A trade-off occurs when a change in a trait increases fitness but is linked to a change in another trait that decreases fitness (Stearns, 1992) – the result overall should maximise reproductive success in the face of existing constraints. In the case of *Paranthropus*, early weaning might result in earlier reproductive maturity but if combined with faster growth overall might also result in a smaller adult body size which would be disadvantageous as a defence against predators. But if predator pressure were high, selection would favour more rapid growth and earlier attainment of adult body size to increase the chance to avoid predation. Trade-offs exist both in individual life history strategies (e.g., between offspring size vs growth, offspring growth vs survival, or maternal current vs future reproduction) and between immature and maternal life history strategies (e.g., between parental vs offspring survival, parental growth (of young adults) vs offspring growth) and trade-offs can involve more than two factors (Stearns, 1992). In extant primates, trade-offs have been identified involving food processing, socioecological factors, demography and mortality profiles, and other factors (Godfrey, et al., 2001; Isbell, et al., 2009; Robbins & Robbins, 2018; Ross, 1998).

Thus, an assessment of the variation in habitats associated with *Paranthropus* fossils is a critical factor in reconstructing *Paranthropus* life history in comparison to other early hominin taxa, and in understanding life history variation within the genus itself. As noted earlier, *Paranthropus* habitats were generally more open than for *Australopithecus* or for extant apes, but may have included riverine forests, open woodland and bushland, edaphic grassland, and deltaic and floodplain habitats (Reed, 1997; Wood & Strait, 2004). This suggests that through the range of potential *Paranthropus* habitats there would have been considerable variation in the availability, distribution and quality of food items, and the type and number of predators. Other factors such as choice of sleeping sites, presence of water sources, and socioecological factors are important but less tangible in the fossil record. All the above are potentially affected by seasonal variability. The range of habitat variation between and within different regions is also consistent with the observed variation in some aspects of *Paranthropus* life history between East and South African species.

It follows that suggested scenarios for *Paranthropus* life history should account for differences in environmental risk among different populations occupying different geographic and habitat areas. Considering both diet resources and predator pressure, the following somewhat speculative scenarios can be presented:

*Paranthropus* fed in a generally open, variable environment, and at least some of the food resources were low-quality (fibrous, etc). Others such as USOs and termites would be widely dispersed and thus limited in availability and require special learned skills to procure. Thus, immatures would be at a competitive disadvantage compared to older individuals for acquiring these foods and would likely consume them in much lower quantities. Maternal investment would likely be high in order to assist and provision younger offspring, but this may be limited to avoid depleting their own food resources. Patchiness, seasonality and competition for food resources during and after the weaning process would select for slower somatic and reproductive maturation of immatures, but food processing requirements might require precocity of dental endowment as reported for folivorous subfossil lemurs. This might select for differences in timing of crown formation (earlier initiation or shorter CFTs) and early permanent tooth emergence. This would involve a trade-off between different aspects of growth and maturation of immatures and maternal investment, as well as between an individual's slow somatic growth and precocious dental investment.

Based on palaeoenvironmental reconstructions and age-at-death profiles from fossil assemblages, *Paranthropus* was subject to various degrees of predation pressure, which would impact on both immature and young adult mortality. This would put into play a trade-off between: a) increasing immature survival through faster rates of development (including earlier weaning?) to increase body size and to achieve independence earlier as a defense against predators; and b) increasing young adult survival for future reproduction through decreased maternal investment so that they can divert resources to achieving their final, larger body size and to allow future reproduction in the face of the risk of predation.

Thus, *Paranthropus* life history trade-offs would be structured by selection relating to competition for different food resources, predation pressure, degree and duration of maternal investment, and aspects of both somatic and dental growth and maturation of immatures. Some of these appear to be in conflict, such as selection for slower growth to avoid feeding competition vs. more rapid growth to attain adult body size to minimise predator risk. This

would result in a complex network of potential variation in life history strategies determined by variation in habitat and food resources, both between broad regions such as East and South Africa, and also within each region due to palaeohabitat variation between site localities. This interpretation is similar to that of Antón and Kuzawa (2017; also Kuzawa & Bragg, 2012) with regard to the effect of morphological and developmental plasticity in *Homo erectus* populations throughout Africa and Asia. It also appears consistent with the variation between *P. boisei* and *P. robustus* in reconstructions of craniodental morphology, dietary ecology, crown formation times, and M1 emergence – there may not be a single consistent ‘*Paranthropus* life history schedule’.

Unfortunately, one big challenge in confirming the likelihood of any such details is that many of these ecological and life history features do not fossilise and any reconstructed scenario will remain necessarily speculative until new methods are developed to produce the relevant data or their proxies.

*Extant primate life history.* The review of evidence presented above indicates the complexities in reconstructing and understanding the range of factors involved in life history variation in hominins and other primates. In contrast to the ‘fast-slow continuum’ model, some studies have demonstrated a dissociation between dental and somatic ontogeny schedules, for example some subfossil lemurs demonstrate a precocity in dental eruption but not somatic growth compared to other species of similar body size (Godfrey et al., 2003), and the African *Homo erectus* KNM-WT 15000 partial skeleton exhibits a higher than expected proportion of adult body mass and stature attainment relative to dental age (Dean & Lucas, 2009). Observations such as these indicate that dental and body size growth are under different selection regimes relating to diet, predation and other ecological risk factors that vary among species, and perhaps populations. Rather than a ‘slow-fast continuum’, or any single driver of life history variation, variation in life history strategies seems better described as ‘modular’ with selection acting on different traits such as dental development, somatic growth or reproductive maturity relatively independently. This concept has been discussed by Leigh & Bernstein (2006) to describe variation in baboon life history, and fits well with explanations of life history variation in extant and subfossil lemurs (Catlett et al., 2010; Schwartz et al., 2002), as well as the concept of plasticity in hominin life history strategies developed by Kuzawa and colleagues (Antón & Kuzawa, 2017; Kuzawa & Bragg, 2012). Perhaps the key question about *Paranthropus* life history is why a primate characterised by its large body (and brain) size would complete at least some life history events at an earlier age compared to other extinct hominins or extant apes.

Figure 31.2 presents box and whisker plots of key life history traits in primates, including gestation length, weaning age, age of first birth, and age of sexual maturity to compare the median and distribution of each variable in relation to mean adult body size and trophic level.

<INSERT FIG 31.2 ABOUT HERE – BOX PLOTS>

The plots were constructed using extant primate data available from PanTHERIA (Jones et al., 2009), which includes a range of developmental life history variables (but none describing dental development), mean species body size, and trophic level (herbivore, omnivore, or carnivore) for 376 primate species (the sample is substantially smaller for each of these plots due to the ubiquitous problem of missing data for variables selected).

Multifactorial ANOVA analysis demonstrated that the means for each life history variable are significantly different ( $p \leq 0.05$ ) among adult body size and diet categories for most but not all comparisons. This suggests that there is at least a general tendency for these life history events to occur at earlier ages in herbivorous (lower quality diet) primates compared to omnivores (higher quality diet), and such differences are greater in the larger body size categories. However, it is important to consider the observation that for many comparisons the ranges overlap so that some herbivores and omnivores attain a particular developmental marker at similar ages.

Table 31.6 presents Pearson's correlations between the key life history traits in the PanTHERIA data set for primates. These correlations are generally strong, but none are equivalent to the extremely strong relationships reported for brain size and M1 emergence age in primates ( $r=0.98$ ) by Smith (1989) and others. However, 10 of 21 correlations obtained were equal or greater than 0.75 and statistically speaking are 'strong correlations'. Even among such 'strong' correlations as much as 25% of the observed variation must be related to other factors – perhaps indicating the effect of life history trade-offs and other factors.

Reflecting some of the issues noted above, these analyses are of limited scope – the trophic category 'herbivore' does not make the important distinction between folivores and frugivores, and body size represents the mean body size of adult males and females, not female body size which is more meaningful in a life history context. Nevertheless, the plots do indicate that diet quality is a significant factor in explaining variation in life history timing in primates. By extension, the 'life history explanation' for early maturation in *Paranthropus* is that its diet is more likely to have consisted of significant amounts of *low-quality* food items, which would exclude at least some hard object food sources.

Figure 2. Boxplots of (a) gestation length, (b) age at weaning, (c) attainment age of sexual maturity, and (d) age at first birth in extant primates (all in days) using data from PanTHERIA (see text). All life history variables are plotted by mean adult body weight categories and coded by trophic level (diet) category. Herbivores include both folivores and frugivores.

Figure 2a.

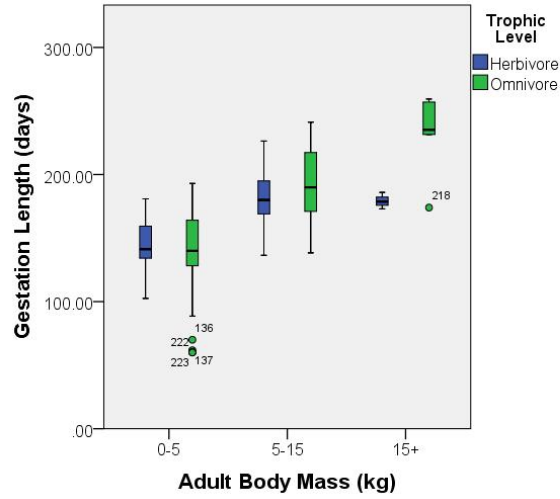


Figure 2c.

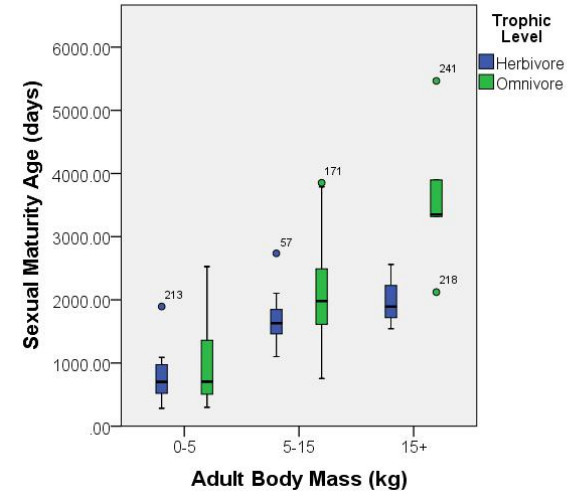


Figure 2b.

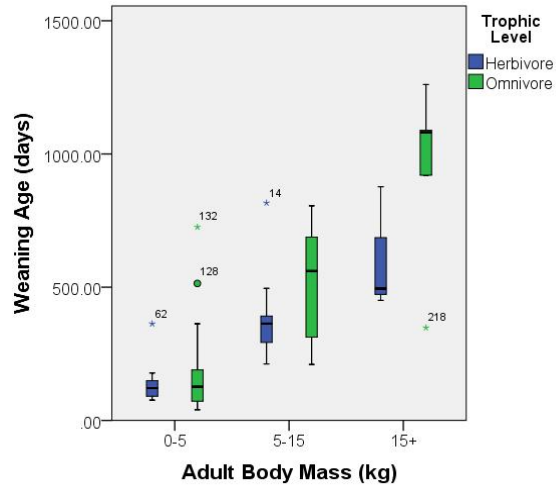


Figure 2d.

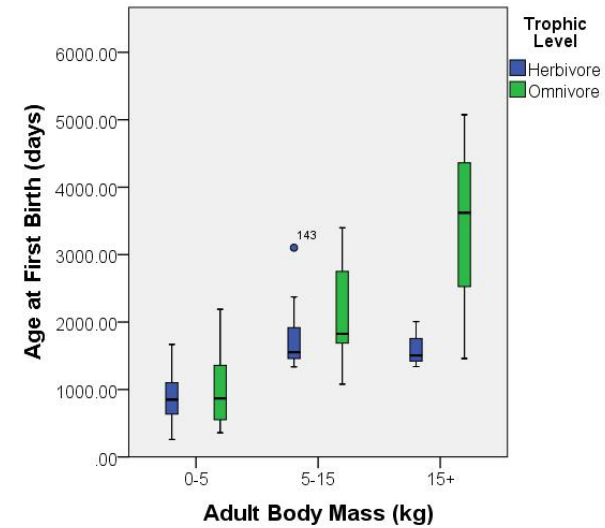




Table 31.6. Pearson Correlations for life history variables in extant primates from the PanTHERIA database (see text). These are generally not as strong as those reported elsewhere (e.g., Smith, 1989) for correlations for brain size and M1 emergence age, but correlations above  $r=0.75$  (bold) are considered to indicate strong relationships between the variables indicated. Also note that correlations for adult body size were not strong, but in the PanTHERIA dataset body size is the mean body mass of adult male and female specimens for each species.

|                                |                     | <b>Adult Body Mass (g)</b> | <b>Age at First Birth (y)</b> | <b>Gestation Length (d)</b> | <b>Interbirth Interval (d)</b> | <b>Maximum Longevity (m)</b> | <b>Sexual Maturity Age (d)</b> | <b>Weaning Age (d)</b> |
|--------------------------------|---------------------|----------------------------|-------------------------------|-----------------------------|--------------------------------|------------------------------|--------------------------------|------------------------|
| <b>Adult Body Mass (g)</b>     | Pearson Correlation | 1                          |                               |                             |                                |                              |                                |                        |
|                                | Sig. (2-tailed)     |                            |                               |                             |                                |                              |                                |                        |
|                                | N                   | 265                        |                               |                             |                                |                              |                                |                        |
| <b>Age at First Birth (y)</b>  | Pearson Correlation | .669**                     | 1                             |                             |                                |                              |                                |                        |
|                                | Sig. (2-tailed)     | .000                       |                               |                             |                                |                              |                                |                        |
|                                | N                   | 103                        | 103                           |                             |                                |                              |                                |                        |
| <b>Gestation Length (d)</b>    | Pearson Correlation | .561**                     | <b>.768**</b>                 | 1                           |                                |                              |                                |                        |
|                                | Sig. (2-tailed)     | .000                       | .000                          |                             |                                |                              |                                |                        |
|                                | N                   | 146                        | 94                            | 146                         |                                |                              |                                |                        |
| <b>Interbirth Interval (d)</b> | Pearson Correlation | .644**                     | <b>.753**</b>                 | .660**                      | 1                              |                              |                                |                        |
|                                | Sig. (2-tailed)     | .000                       | .000                          | .000                        |                                |                              |                                |                        |
|                                | N                   | 109                        | 90                            | 102                         | 109                            |                              |                                |                        |
| <b>Maximum Longevity (m)</b>   | Pearson Correlation | .638**                     | <b>.762**</b>                 | .603**                      | .588**                         | 1                            |                                |                        |
|                                | Sig. (2-tailed)     | .000                       | .000                          | .000                        | .000                           |                              |                                |                        |
|                                | N                   | 125                        | 92                            | 106                         | 89                             | 126                          |                                |                        |
| <b>Sexual Maturity Age (d)</b> | Pearson Correlation | .636**                     | <b>.926**</b>                 | <b>.764**</b>               | <b>.772**</b>                  | <b>.776**</b>                | 1                              |                        |
|                                | Sig. (2-tailed)     | .000                       | .000                          | .000                        | .000                           | .000                         |                                |                        |
|                                | N                   | 109                        | 90                            | 104                         | 92                             | 97                           | 110                            |                        |
| <b>Weaning Age (d)</b>         | Pearson Correlation | .649**                     | <b>.782**</b>                 | .742**                      | <b>.826**</b>                  | .660**                       | <b>.823**</b>                  | 1                      |
|                                | Sig. (2-tailed)     | .000                       | .000                          | .000                        | .000                           | .000                         | .000                           |                        |
|                                | N                   | 119                        | 97                            | 106                         | 94                             | 97                           | 97                             | 119                    |

\*\* Correlation is significant at the 0.01 level (2-tailed).

Future research is clearly needed to test how a range of life history variables respond to differences in diet quality and how they might vary in relation to the aspects of developmental timing and life history. At this stage, it should be expected that these factors involve a considerable amount of variation at the species level. A collaborative effort to produce a large and carefully selected data set and to analyse it in a consistent and appropriate manner is needed (Borries, Gordon, & Koenig, 2013; Jones et al., 2009). Key to this effort is to develop approaches to tie research in extant primate life history to data extractable from fossils.

## CONCLUSION

To the extent that ontogenetic and life history variation is a component of a species' adaptive strategy, the reconstruction of *Paranthropus* life history presented is consistent with general features of *Paranthropus* palaeobiology involving a high-risk environment and low quality dispersed dietary resources (Bromage, 1990; Kelley & Schwartz, 2012; Kuykendall, 2003; Lee, 2012; Wood & Constantino, 2007), and drawing on explanations of life history variation among extant primate species (Godfrey et al., 2001; Leigh, 1994; Ross, 1998).

The *Paranthropus* life history model presented suggests that key developmental events during a juvenile's lifetime occurred at younger ages and over shorter durations of time compared to other hominins and to all extant apes, constituting a uniquely adapted life history strategy in the genus. The evidence that not all life history events occurred at younger ages (e.g., M1 emergence age vs CFTs) is compelling, and this most likely reflects the effect of life history trade-offs involving environmental risks relating to the effect of diet, maternal investment and predator pressure on growth and maturation schedules. Perhaps even more interesting is the evidence that the impact of these environmental risk factors appears to differ between habitats in East and South Africa, and perhaps even between *Paranthropus* sites within each region. Given that *Paranthropus* diets are different from extant ape diets, and that predator pressure is not a significant factor at least in *Gorilla* and *Pongo*, it is difficult to construct a completely coherent life history reconstruction for *Paranthropus* at this stage.

These details of the *Paranthropus* life history schedule are generally compatible with what we know of life history across primates for species that consume a largely folivorous, low-quality diet. However, this relationship has recently been challenged for Asian colobines and macaques, as well as some subfossil lemurs and is likely to be more complex. One relevant factor for interpreting and confirming such research is that the available comparative data sets used in primate life history research are widely regarded as problematic and largely do not include variables that are relevant for interpretation of fossil assemblages. Future research efforts to improve available primate life history data sets and to define and clarify key variables meaningful to life history reconstruction in both extant and extinct species would significantly improve life history inferences in palaeoanthropology.

This review also supports the view that *Pan* (an omnivore) is not the best model for reconstructing *Paranthropus* life history, even if it is more relevant to other hominin species, or in a broader comparative perspective. Among apes, *Gorilla* (herbivore) and *Pongo* (frugivore) are likely to be more appropriate models, and both exhibit higher levels of sex dimorphism and bimaturation in males. The unique combination of high sex dimorphism in body size and the lack of dimorphism in the canine crown is a unique and puzzling aspect of *Paranthropus* palaeobiology. These may be important components of the *Paranthropus* life history adaptation for which information is currently lacking.

Life history research in palaeoanthropology should draw more closely on extant primate research in order to begin testing a more comprehensive life history framework for *Paranthropus* and other extinct hominins in an evolutionary context. In particular, aspects of mortality risk, dietary ecology, and social organisation are known to impact strongly on life history strategies in extant primates. Continued research employing a deeper comparative approach with extant primates would illuminate the range of possible solutions to the different challenges faced in the context of life history adaptation. Even within a single genus such as *Paranthropus*, it no longer seems realistic to expect a common life history strategy that characterises all species.

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