Slow it down: evolution of human metabolism over two million years.

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Abstract

Previous estimates of the total energy expenditure (TEE) of fossil hominins have assumed vigorous to very vigorous physical activity levels (PALs) when reconstructing their daily energy budgets. However, these PALs are not common for current hunter-gatherers and other subsistence economy populations. The purpose of this study is to reassess the evolution of TEE in the *Homo* genus by applying predictive equations recently evaluated based on body mass (BM). These equations were applied to 112 individuals of *Homo erectus sensu lato*, *Homo antecessor*, Mid-Pleistocene *Homo, Homo neanderthalensis* and fossil *Homo sapiens*. Our results suggest that the use of vigorous PALs for past hominins would overestimate their daily energy budgets by approximately 8.4 MJ/day compared to current populations. Furthermore, metabolic acceleration and deceleration linked to changes in BM have likely occurred over the past 2 Mya. These shifts could have been related to the ability of certain species to use exosomatic energy. The use of the predictive models presented here can be an asset to modeling past energetic dynamics and populations' ecology.

Keywords: Total energy expenditure, *Homo*, physical activity levels, body mass.

1. Introduction

The famous quote of Dobzhansky, "nothing in biology makes sense except in the light of evolution" (Dobzhansky, 1973), was nuanced by Wallace (2010) adding that "nothing in biology exists without energy flux". Energy has a central role in understanding survival dynamics and the interaction between every organism and its environment (McNab, 2002). Therefore, the evolution of energy acquisition and use has been the focus of research for many decades (Leonard & Ulijaszek, 2002), including in anthropology (Ocobock, 2020; Pontzer, 2015b; Urlacher, 2023).

Advances in the knowledge of human metabolism and how energy is partitioned to maintenance, physical activity, growth, and reproduction (Leonard, 2018) have encouraged many researchers to estimate the costs of survival for extinct hominins (among others, Aiello & Wells, 2002; Churchill, 2014; Froehle & Churchill, 2009; Leonard & Robertson, 1997; MacDonald et al., 2009; Snodgrass & Leonard, 2009; Steegmann et al., 2002; Steudel-Numbers & Tilkens, 2004; Wall-Scheffler, 2012). The aforementioned research has always been conducted under an additive conception of the human energy budget (Leonard & Robertson, 1997; Pontzer, 2017), known as the "factorial method". Under this framework, the total energy expenditure (TEE) of an individual is the product of resting metabolic rate (RMR) and a physical activity level (PAL) (FAO/WHO/UNU, 2004). The RMR represents the minimum amount of energy required to sustain vital functions in a rested state (Fernández-Verdejo et al., 2024). PAL is obtained by dividing TEE by RMR. Therefore, PAL is a multiplier reflecting the level of activity ranging from 1.3 for very sedentary lifestyles to >3.0 for extremely vigorous. Vigorous to very vigorous PALs (>2) were usually assumed for extinct hominins based on ethnographic estimations (Shephard & Rode, 1996; Steegmann et al., 2002). This was especially the case for Neanderthals (*Homo neanderthalensis*; King, 1864), for which TEE was historically estimated to be in the range of 2 to 3 times their RMR (Churchill, 2006; Hockett, 2012; Snodgrass & Leonard, 2009). In addition, Snodgrass and Leonard (2009) also emphasized the significant contributions of a highly meat-based diet and severe thermal stress in influencing Neanderthal energy demands. As a result, Snodgrass and Leonard (2009) concluded that Neanderthal males' TEE would vary between 16.7 and 29.3 MJ/day (4-7,000 kcal/day) and between 12.6 to 20.9 MJ/day (3-5,000 kcal/day) for females. In contrast, recent evidence suggests that Neanderthals had a more varied diet which included plant matter (Fiorenza et al., 2020; Hardy et al., 2022; Henry et al., 2014; Power et al., 2018; Sistiaga et al., 2014), and not all faced severe thermal stress, particularly in temperate climates like the Mediterranean (El Zaatari et al., 2016; Fiorenza et al., 2015; Pomeroy, 2023).

An alternative theoretical framework suggests that, as energy is a limited resource, many adaptative strategies have evolved to ensure the maintenance of the daily energy budget within a narrow range (Drent & Daan, 1980; Peterson et al., 1990; Pontzer, 2015a). Humans may then adapt their behavior and/or physiology through compensatory mechanisms to reduce the cost of other tasks when physical activity increases (Constrained or Compensatory models of TEE) (Dolan et al., 2023; Halsey, 2021; Pontzer, 2015a, 2025). As Life History Theory and the first law of thermodynamics suggest, the energy that is dedicated to one biological task is not available for others (Charnov & Berrigan, 1993; Stearns, 1989). Therefore, alternatives to a factorial method for TEE calculation may be more appropriate including for the estimation of extinct hominins' TEE.

Recent investigations using the gold standard doubly labeled water (DLW) technique to measure TEE (Westerterp, 2017) have shown little to no difference in energy needs across adult populations with different lifestyles, outdoor temperature exposure, and physical activity levels (Dugas et al., 2011; Pontzer et al., 2016b; Pontzer et al., 2015; Urlacher et al., 2019; Zhang et al., 2022), as well as among captive nonhuman primates and wild mammals (Pontzer et al., 2014). Most importantly, the average PAL for human populations with subsistence economies corresponds to a moderately active lifestyle (Lieberman et al., 2021) (PAL ~1.89, see references in Table 1). This suggests that daily vigorous to very vigorous PALs may not have been the norm for Pleistocene hominins (Berger et al., 2023; Lieberman, 2015; O'Keefe & Lavie, 2021; Shave et al., 2019). In this sense, when reconstructing past hominins' TEE, the health and metabolic consequences of extreme levels of physical activity for current humans should be considered (Areta, 2023; Ellison, 2008; Loucks, 2001).

Hence, we propose the use of predictive equations based on body mass (BM), developed using DLW (i.e., Vinken et al., 1999; Pontzer et al., 2021) to estimate the TEE for extinct populations. The accuracy of these equations has been recently evaluated (Prado-Nóvoa et al., 2024). These TEE estimations help model and understand the complex interactions between metabolism, environmental factors, and behavior, offering new insights into hominin adaptation and survival strategies (Froehle et al., 2013). The use of these equations for extinct hominins is supported by two observations. First, there is a strong correlation between energy needs and BM across mammals and, particularly, primates (McGrosky & Pontzer, 2023; Pontzer et al., 2014). Second, it has been suggested that the trade-offs regulating modern human energy budgets evolved in early Pleistocene hominins (Pontzer, 2017) largely due to the increase in brain size within the *Homo* (Linnaeus, 1758) genus (Antón et al., 2014). Specifically, a significant metabolic shift towards a modern human pattern is thought to have occurred in *Homo erectus* (Dubois, 1894), driven by several key evolutionary changes, including increases in brain and body size, shifts in dietary patterns, improvements in thermoregulation, and adaptations for long-distance walking or endurance running (Aiello & Wheeler, 1995; Bramble & Lieberman, 2004; Leonard & Robertson, 1997; Morin & Winterhalder, 2024; Pontzer, 2017; Yegian et al., 2024).

Accordingly, the purpose of the present analysis was to estimate the TEE along the evolutionary timeline of the *Homo* genus using a database of more than 100 individuals. Shifts in body size and both sexual dimorphism and the consequences for hominins' daily energy budgets will be explored. In addition, alternative approaches based on body composition estimations will be evaluated. While body mass is the common predictor in most models, we applied multiple equations to assess how parametric differences (slopes and intercepts) may influence absolute TEE trends across hominin evolution. We advance the hypothesis that TEE estimates over time will not only reflect body size changes but also reveal crucial metabolic adaptations that underpinned the evolutionary success of the *Homo* genus. These estimations provide key insights into how metabolic flexibility, alongside the use of external energy sources such as fire and tools, shaped *Homo* species' biology. By assessing TEE, we can better understand the energy demands that influenced survival strategies, enabling *Homo* species to adapt to diverse environments and thrive through evolutionary time.

2. Materials and Methods

2.1. Current subsistence populations' physical activity levels and total energy expenditure

Gurven et al. (2013) was used as a reference to obtain the physical activity levels (PAL) of different societies with subsistence economies, including adult hunter-gatherers, agriculturalists, farmers, and pastoralists (primary sources of information were mentioned in Table 1 when available). The goal is not to precisely determine the PALs of extinct hominins, but to offer a plausible estimate based on current subsistence populations. Including a broad range of subsistence economies beyond hunter-gatherers helps provide a more comprehensive view of typical activity levels in these communities. Although the tasks of farmers differ from those of hunter-gatherers, a wider range of physical activities that extinct hominins might have engaged in under different environmental conditions could be captured (Kraft et al., 2021). The latter and the general PALs in Table 1 support the need to adjust expectations regarding the PALs of extinct populations.

The body mass (BM) of these populations and the total energy expenditure (TEE) of five of them were obtained from the literature (Table 1). TEE relied only on measurements of free-living energy requirements using the gold standard method, the doubly labeled water (DLW) technique (Westerterp, 2017). For comparison, BM, PAL, and TEE of industrialized populations were obtained from Pontzer et al. (2012). Of note, the PALs in Table 1 were derived using a combination of methods, including accelerometry, DLW, and the factorial method (see details in the table). Although results may differ between methods, integrating them into the table offers a more comprehensive view of the PALs across various communities.

2.2. Hominins sample

Ninety-four individuals with estimated sex and BM (kg) were extracted from the database published by Will et al. (2017). The estimated sex was retrieved from the literature (see details in Supplementary Online Material (SOM) Table 1) for eighteen other individuals for whom BM was available. Height (cm) was also extracted from Will et al. (2017) when available. We generated a database with a total of 112 hominins with estimated BM and sex, 86 of them also had a reported height available. Sources of body size estimation were provided by Will et al. (2017) and were all based on lower limb long bones, foot bones, or pelvises (see Will et al. 2017 Supplementary Material). BM and height were only updated for the association between Femur X + Pelvis 1 of the Sima de los Huesos hominins following Carretero et al. (2023) and Carretero et al., (2024). Qafzeh 9 individual was referred as a female by Friedl et al. (2016) and as male by Coutinho-Nogueira et al. (2021). Femur XII and XIII from Sima de los Huesos were reported as males by Will et al. (2017), but as females by Carretero et al. (2023). In these cases, the analyses were repeated considering each sex.

Will et al. (2017) reported only adult individuals in their database. An approximate age at death was obtained from the literature for most of the individuals (see details in SOM Table 1). When age was provided as a range or more than one age was found, the average was calculated. When unavailable, a minimum age at death of 20 years was assumed (n=56). When authors referred to “older adult”, an age of 35 years was assumed (see details in SOM Table 1).

Five different taxonomical categories of the *Homo* genus were included in our analyses, ranging from 2 to 0.011 Mya ago: *Homo erectus sensu lato*, *Homo antecessor* (Bermúdez de Castro et al., 1997), Mid-Pleistocene *Homo*, *Homo neanderthalensis* and fossil *Homo sapiens* (Linnaeus, 1758). We followed Will et al. (2017) categories for narrow taxonomic groups. Mid-Pleistocene *Homo* included Sima de los Huesos (SH) hominins in our analyses. Despite the existing debate on SH hominin's assignation as early *H. neanderthalensis* or other paleodeme (i.e., Arsuaga et al., 1997; Stringer, 2012; Lockey et al., 2022), using a broader category allowed us to simplify our analyses and increase the sample size per group. Determining if SH hominins should be considered early *H. neanderthalensis* or another closely related group is beyond the scope of this manuscript (see Arsuaga et al., 2014 among others) and we considered it more parsimonious to assign them to the Mid-Pleistocene *Homo* category following Will et al. (2017). Other *Homo* species, like *H. habilis* (Leakey et al., 1964), were not considered for analyses due to a proposed shift in metabolism related to increased brain size and modern human-like body proportions since *H. erectus* (Bramble & Lieberman, 2004; Lieberman, 2015; Pontzer, 2017). For the same reason, specimens with a different bauplan, e.g., *H. naledi* (Berger et al., 2015) and *H. floresiensis* (Brown et al., 2004) characterized by markedly small body and brain size, were also excluded.

2.3. Total energy expenditure estimation based on BM and data analysis

The TEE of the adult hominin sample was estimated with four different equations based on BM. To facilitate comparison with the classic literature, we first used the factorial method, estimating the resting metabolic rate (RMR) by the FAO equation according to age and sex (FAO/WHO/UNU, 2004) and multiplying the result by different physical activity levels (PALs): 1.89= the average for subsistence economies populations (Table 1); 2, 2.5, and 3=vigorous PALs commonly applied to extinct hominin species, like Neanderthals (Churchill, 2006; Froehle & Churchill, 2009). After the factorial method, Leonard and Robertson's (1997) formula and Pontzer et al. (2021) equation, both based on BM, and Vinken et al. (1999) model using BM and height, were applied. The rationale for applying these equations is that the Leonard and Robertson (1997) model, which was based on a sample of humans and nonhuman primates (Leonard & Robertson, 1997), has been previously applied to estimate Neanderthals' TEE (Churchill, 2006). Additionally, the accuracy of the Pontzer et al. (2021) and Vinken et al. (1999) models were recently evaluated in predicting the TEE in a sample of adults varying in physical activity levels (Prado-Nóvoa et al., 2024). These equations are also advantageous because they rely on simple characteristics such as BM, height, sex, and age, without requiring specific PALs to estimate TEE (Pontzer et al., 2016b). Using multiple equations allows for comparisons between methods that vary in how they incorporate BM and other physiological factors. Furthermore, this approach allows us to determine if trends in metabolic changes over time are consistent despite the model used. The details of the models applied are included in SOM Table 2. Height was not available for all the specimens and, as such, the Vinken et al. (1999) equation could only be applied to 86 of the 112 individuals (SOM Table 1).

Using the average TEE for subsistence economies as a reference (Table 1), the difference with the average TEE obtained from the predictive equations for each hominin species was calculated. The prediction of TEE was compared between equations with a one-way repeated-measures analysis of variance (ANOVA) with the Bonferroni post-hoc test. The Vinken et al. (1999) equation was used as the comparison reference because it was the most accurate in predicting the TEE in a sample of current humans (Prado-Nóvoa et al., 2024).

To avoid redundancy, the remainder of the statistical analyses were only carried out with the TEE obtained from Vinken et al. (1999) model. Differences in the TEE among species were evaluated by ANOVA and visualized using a box and whisker plot. Differences between sexes were analyzed for each species using a student's t-test and visualized with a box and whisker plot. The analysis of sex-specific TEE is based on the sexual dimorphism in hominin body size (Ruff, 2002), which likely influenced energy allocation, reproduction, and survival strategies. Estimating TEE by sex helps us understand how these differences impacted metabolic rates and adaptation in extinct species. All the statistical analyses were carried out with Statgraphics Centurion 19.

2.4. Additional estimations of total energy expenditure based on body composition

Fat-free mass (FFM) is a better predictor of energy expenditure than body weight (Johnstone et al., 2006). As such, we performed additional analyses to predict TEE in fossil hominins using a range of fat mass (FM) for current populations that is consistent with normal or healthy weight (FAO/WHO/UNU, 2004). The ranges of FM for current humans were used based on two assumptions. First, it has been proposed that the larger encephalization during *Homo* evolution was linked to an increase in the body fat percentage compared to other primates (Navarrete et al., 2011; Pontzer et al., 2016a). Second, these ranges of FM are common in subsistence economy populations (Table 1) which allows them to keep their regular physical activity levels without jeopardizing reproduction (Sadhir & Pontzer, 2023).

Average body masses for each sex (Table 2) were used as a reference to apply the ranges of body composition. TEE was estimated with two equations. First, the Pontzer et al. (2021) equation for TEE based on FM and FFM. The accuracy of this model was recently tested in a population of current humans (Prado-Nóvoa et al., 2024). Second, the Pontzer et al. (2021) model to predict RMR, multiplied by a PAL of 1.89. Previous research (Prado-Nóvoa et al., 2023) showed that this equation was remarkably accurate in a sample of current humans.

The results obtained with these equations were compared to those obtained with the Vinken et al. (1999) equation.

3. Results

3.1. Estimations based on BM

The compilation of BM, PAL, and TEE for subsistence economy populations is shown in Table 1. The average individual within this lifestyle would be represented by a BM of 56.7 kg, a PAL of 1.89, and a TEE of 11.4 MJ/day (2,726 kcal/day). The average estimated BM size for past hominins was larger than for current populations, ranging from 76 kg for the *H. antecessor* specimen, to 66.4 kg for fossil *H. sapiens* (Table 2).

The estimated TEE for past adult hominins derived from BM differences were generally higher (by 0.8 to 2.9 MJ/day or 203-715 kcal/day) than the average for current subsistence economy populations (i.e., Vinken et al. (1999) equation in Table 3, results in Table 4, and sex comparisons in Table 5). The Leonard and Robertson (1997) model resulted in lower predicted TEE for extinct hominins than current humans, and Pontzer et al. (2021) provided TEE levels similar to current humans despite clear differences in BM (Table 4). When predictive equations were compared, only the estimated RMR and a PAL=1.89 provided systematically similar results to the Vinken et al. (1999) model (p-value>0.05). Although the average TEE was lower in *H. neanderthalensis* and fossil *H. sapiens* compared with other hominins (Figure 1), there were no significant differences in TEE among species (f= 1.91; p-value>0.05) (Figure 1 and Table 3).

The use of vigorous PALs (2.5-3.0) results in TEE ranging from 16.7 to 20.9 MJ/day (4,000 to 5,000 kcal/day) (Table 5) or approximately 8.4 MJ/day higher (~40-50%) for past hominins compared with current humans of non-industrialized economies (Table 4). Significant sex differences in TEE due to BM differences were detected for Mid-Pleistocene *Homo* (t= -3.53; p<0.01), *H. neanderthalensis* (t= -4.67; p<0.01), and fossil *H. sapiens* (t= -6.19; p<0.01) (Table 5).

Despite the variations between equations, the results consistently indicate a trend toward a metabolic acceleration until the Middle Pleistocene, followed by a subsequent metabolic deceleration, due largely to differences in BM across species (Table 3 and Figure 1).

3.2. Estimations based on body composition and comparisons to BM equations

The Pontzer et al.(2021) equation for TEE based on FM and FFM resulted in lower estimates for females than the Vinken et al. (1999) model (Figure 3 and Table 6). For males, this model resulted in slightly higher TEE for Mid-Pleistocene *Homo*, *H. neanderthalensis*, and fossil *H. sapiens*, particularly at the lower range of FM (12%) (Figure 3 and Table 6).

The Pontzer et al. (2021) model to predict RMR, multiplied by a PAL of 1.89, resulted in TEE values within or very close to the ranges of the TEE predicted with the Vinken et al. (1999) model for females (Figure 3 and Table 6). For males, leaner individuals (12% of FM) of Mid-Pleistocene *Homo*, *H. neanderthalensis*, and fossil *H. sapiens* could have a TEE approximately 1.7 MJ/day (~400 kcal/day) higher than predicted by Vinken et al. (1999) equation (Figure 3 and Table 6). The estimated TEE values remained less than those obtained if very vigorous PALs were considered for these species (Tables 3, 4, and 5).

The same trends in metabolic changes detected with the BM equations were seen when the models using body composition were applied (Table 6 and Figure 3).

4. Discussion

The main finding of the present analysis is that, consistent with differences in BM, the TEE of past adult hominins tended to be somewhat higher than for modern subsistence economy populations (Tables 3 and 4). Similar results were obtained when a PAL of 1.89 was used to estimate TEE (Tables 3 and 4). Although recently challenged, the use of additive models may be insightful for moderately active lifestyles (Pontzer et al., 2016b). Nonetheless, although more validation studies are needed, we propose using the Vinken et al. (1999) model as the reference to estimate past hominins' daily energy demands given its use of readily available variables and its superior accuracy in predicting TEE in a sample of current humans (Prado-Nóvoa et al., 2024). We believe it unlikely that TEE would have been lower for extinct hominins than current subsistence economy groups (Table 1), as predicted by Leonard and Robertson (1997), or as close as predicted by Pontzer et al. (2021) equation given their larger BM. Churchill (2006) suggested that Leonard and Robertson's model may underestimate TEE due to the inclusion of captive nonhuman primates with lower energy demands relative to BM (Leonard & Robertson, 1997; Pontzer et al., 2014). The underestimation obtained with this model is consistent with a metabolic acceleration in *Homo* evolution compared to other apes (Pontzer et al., 2016a; Yegian et al., 2024). On the other hand, BM had a smaller contribution to TEE in the Pontzer et al. (2021) model (as indicated by the slope in SOM Table 2), which could explain the lower estimates obtained using this equation. This equation underestimated the TEE in a sample of current humans as well (Prado-Nóvoa et al., 2024).

Leaner males (12% of FM) of Mid-Pleistocene *Homo*, *H. neanderthalensis*, and fossil *H. sapiens* may have had a higher TEE than predicted by the Vinken et al. (1999) equation (Figure 3 and Table 6). The underestimation for hominin females with Pontzer et al. (2021) equation for TEE was also observed in a sample of current females (Prado-Nóvoa et al., 2024). The slight overestimation for hominin males TEE was also found for current *H. sapiens* males (Prado-Nóvoa et al., 2024). The model by Pontzer et al. (2021) to predict RMR with body composition was remarkably accurate in a sample of current humans (Prado-Nóvoa et al., 2023). If multiplied by a PAL of 1.89 to obtain a TEE, leaner males of certain species may have had a higher TEE than predicted by the Vinken et al. (1999) model (Figure 3 and Table 6). However, until a better approximation of body composition in extinct populations is available, estimating TEE with body size seems more parsimonious.

We hypothesize that PALs ≥2 (vigorous to very vigorous) were not common on a daily basis along the *Homo* genus evolution (Berger et al., 2023; Lieberman, 2015; O'Keefe & Lavie, 2021; Shave et al., 2019). The results of a recent study of human metabolism suggest that an alimentary limit may be the primary factor determining the sustainable metabolic ceiling (Thurber et al., 2019), although limits imposed by heat dissipation capabilities cannot be dismissed (Król et al., 2023; Sadowska et al., 2016; Thurber et al., 2019; Zhao et al., 2020). The innate capacity of the digestive system to assimilate adequate calories and nutrients to maintain BM stability may be limiting at ~2.5 times the RMR (Peterson et al., 1990; Thurber et al., 2019). Higher levels of physical activity increase the reliance on somatic fuel reserves, affect reproductive capacity, exercise performance (Dolan et al., 2023; Longman et al., 2023), and bone metabolism, among others (see references in Dolan et al., 2023 and Areta et al., 2023) especially if sustained long term. Higher sustainable PALs (Best et al., 2023; Thurber et al., 2019) may be possible for cyclists and swimmers who may have lower thermoregulatory burdens due to higher convective heat loss, but others may depend heavily on nutritional supplementation with prior gut training and advances in food science (e.g. use of energy hydrogels) (Martinez et al., 2023; Viribay et al., 2020). Although compared to other primates the human diet is characterized by its variety and the preference for energy and nutrient-rich foods (Crittenden & Schnorr, 2017; Pontzer, 2015b), past hominins were unlikely to exceed their sustainable alimentary limits with their available technology, as current elite athletes may do.

Even if the human energy budget is not limited, there would seem to be no obvious survival benefit of extreme PALs as long as energy availability for resource procurement, tools elaboration, leisure, and social time is ensured (Areta, 2023). Although our compilation in Table 1 is based on reduced available data and variability among populations is expected (Gurven et al., 2013), the available evidence suggests that current subsistence economy populations achieve this with a moderately active lifestyle (Lieberman, 2015) (Table 1). Vigorous PALs may, indeed, have detrimental health consequences (Loucks, 2001; Sadhir & Pontzer, 2023). Venkataraman (2023) suggested that the continuous involvement in extraordinarily demanding tasks by past populations is a misconception of how modern populations understand productivity and work time. Instead, hunter-gatherers developed technological and behavioral mechanisms that increased their energy acquisition rates in less time augmenting available time for leisure (Kraft et al., 2021). Avoiding extreme levels of physical activity may have been beneficial not only to minimize energy expenditure (Lee et al., 2016), but also to decrease the risk of starvation (Pontzer, 2015b) and predation (Speakman, 2020). In this sense, Speakman (2020) proposed that certain sedentary behaviors may have been selected to mitigate mortality risks associated with predator exposure or navigating dangerous environments, ultimately enhancing survival.

We suggest that, as hunter-gatherers and other populations do, extinct hominins would avoid living close to their metabolic ceiling, given behavioral, physiological, and anatomical adaptations that were under strong selection to reduce the risk of energy shortfalls (Pontzer et al., 2016a) and predation (Speakman, 2020). Although controversial (see references in Carretero et al., 2018), this perspective is consistent with genetic factors, rather than vigorous physical activity, being the cause of high skeletal robusticity in certain species, such as Mid-Pleistocene *Homo* and *H. neanderthalensis* (Carretero et al., 2018).

In contrast to other apes, human metabolism may have experienced an acceleration that allowed the maintenance of an increase in body and brain size, as well as a faster reproductive pace, without reducing longevity (Pontzer et al., 2016a; Yegian et al., 2024). In contrast, others have shown that human daily energy needs match expectations for mammals based on BM (Westerterp & Speakman, 2008). However, more accurate insights into the evolution of human metabolism can be gained by comparing humans to other apes (e.g., Snodgrass et al., 2007; Pontzer et al., 2016a; Yegian et al., 2024). Further research on the metabolism of wild primates will also improve our understanding of evolutionary differences within genera. Compared to other apes, humans exhibit a unique energetic paradox: a faster reproductive rate combined with a longer lifespan (Isler & van Schaik, 2012). This paradox, likely a derived feature that evolved in early Pleistocene hominins (Pontzer, 2017), involved an increase in both metabolic rate and trade-offs in energy allocation (Pontzer et al., 2016a). As previously suggested, *Homo erectus* underwent a crucial metabolic shift towards a modern human pattern which was driven by factors such as the enlargement of brain and body size, dietary changes, and physical adaptations for endurance activities and improvements in thermoregulation (Aiello & Wheeler, 1995; Kamberov et al., 2018; Pontzer, 2017).

Although we found no significant differences in TEE among species (Table 3), related to shifts in body size (Will et al., 2017), three different trends in metabolic acceleration and deceleration along hominin evolution were possible (Figure 1). First, natural selection favored greater body sizes (Little, 2020) with ecological advantages (Will et al., 2017) and a metabolic acceleration occurring between *H. erectus* and Mid-Pleistocene *Homo*. Subsequently, a second transition occurred towards a reduction in body size until archaic and Holocene *H. sapiens* (Little, 2020; Ruff, 2002; Will et al., 2017) reducing daily energy budgets. The latter transition since the Middle Pleistocene may have been caused by advances in technology and sociability (Henry et al., 2018; MacDonald et al., 2021; Rodríguez-Hidalgo et al., 2017) enhancing hominins' capacity to use exogenous (i.e., use of fire for thermoregulation, tools improvement, communal hunt or cooking to facilitate digestibility and nutrient absorption) instead of endosomatic energy (Kraft et al., 2021; Pontzer, 2021) (i.e., costs of body thermoregulation, higher costs of the digestive system, higher effort in tools elaboration or prey chase). This, in turn, would reduce the selective pressures for bigger body sizes (Vidal-Cordasco et al., 2021). While shifts in body size may have been associated with changes in energy allocation to offset the costs of a larger brain (Aiello & Wheeler, 1995; Froehle et al., 2013), the role of exosomatic energy use in influencing hominin biology offers deeper insights into the energetic dynamics of the past. This perspective enhances our understanding of how external energy sources may have mitigated internal metabolic constraints and, in turn, facilitated adaptations in past human populations. Hominins with a different bauplan, like *H. naledi* and *H. floresiensis*, were not included in our analyses, but their smaller brain and body size may be the result of speciation in specific niches requiring different metabolic adaptations to those estimated for contemporary species (Püschel et al., 2021). Modern industrialized societies seem to be experiencing a third transition with an increase in body size, although there is considerable geographic and socioeconomic variation (Little, 2020). However, their TEE is similar to subsistence economy groups (Pontzer et al., 2012) (Table 1). Decoupling the logical relationship between body size and energy expenditure in this latest trend may be the result of the extraordinary use of exosomatic energy by current populations (Pontzer, 2021) (i.e., fuel, heating/cooling systems, transportation). Given that TEE and physical activity have not decreased significantly in recent decades (Speakman et al., 2023; Westerterp & Speakman, 2008), changes in the food environment and overconsumption may be the primary factors in the rise of current non-communicable diseases, such as obesity (Pontzer, 2021).

Our analysis focuses on physiological trends and a detailed analysis of technological and cultural evolution falls beyond our scope. We suggest that these metabolic shifts may broadly coincide with key periods of innovation in hominin cultural evolution, for example, fire control in the Middle Pleistocene (MacDonald et al., 2021; Roebroeks & Villa, 2011; Wrangham & Carmody, 2010), transitions in stone tool complexity in the Middle and Late Pleistocene (Paige & Perreault, 2024; Režek et al., 2018; Wilkins, 2020), and demographic growth transitions with species coexistence and extinction (Coward & Grove, 2011; Hamilton et al., 2007; Vidal-Cordasco et al., 2023). Our metabolic estimates provide a valuable baseline for future studies to formally test relationships between energetics, cultural innovations, and population dynamics.

Analyses of sex differences in body size supported that recent species have reduced sexual dimorphism compared to younger species in the *Homo* genus (Will et al., 2017). Others have reported similar degrees of sexual dimorphism over time (Ruff, 2002). Body size differences may also lead to different daily energy budgets among sexes. Our results indicated no significant sex differences in TEE for *H. erectus* individuals, but significant differences for Mid-Pleistocene *Homo*, *H. neanderthalensis*, and fossil *H. sapiens* (Table 5). Interestingly, the sex differences in TEE (approximately 1.8 MJ/day) did not change substantially among these late species. Nevertheless, the shift towards a metabolic deceleration after the Middle Pleistocene was evident for both females and males of the different species (Figure 2). Although these results may be relevant for reconstructing social behaviors (Plavcan, 2001) and differential investment in reproductive strategies by sex (Lassek & Gaulin, 2022) in past hominins, caution must be taken due to the small sample size representing some species in our sample (Table 1). Interestingly, greater variability in TEE has been observed in males compared to females, suggesting that distinct evolutionary strategies may have influenced metabolic flexibility between the sexes (Halsey et al., 2022). As the fossil record grows, additional research will be possible.

4.1. Limitations and future research directions

There are several limitations of our analyses that should be considered as potential opportunities for future research. Our dataset includes fossil specimens from multiple species, periods, geographical regions, and ecological contexts, as well as estimations derived from different skeletal elements and predictive equations. These factors, together with the relatively small sample sizes, introduce inherent uncertainties and potential artefacts into our reconstructions. While such heterogeneity reflects the complex evolutionary and ecological diversity of hominins, acknowledging these limitations is essential to appropriately contextualize our findings. The influence of different ecological niches and temperature on metabolism (Ocobock, Soppela, et al., 2021; Sellers et al., 2022) was not explored. Predicting the effect of such seasonal metabolic fluctuations among extinct species has major limitations (Snodgrass & Leonard, 2009), and there are no validated models to predict TEE in humans that include these variables. Several authors have predicted that species adapted to cold climates may have had a TEE approximately 10% higher than those inhabiting temperate climates (Froehle & Churchill, 2009; Sorensen & Leonard, 2001). Cold-adapted populations have higher proportions of subcutaneous fat, but also greater lean mass (Ocobock, 2023; Wells, 2012). Metabolic measurements in extant populations demonstrate higher-than-expected energy needs for these populations but with high interindividual and interpopulation variability in RMR and TEE (Leonard et al., 2005; Ocobock, 2023). More research is needed as measurements of TEE are more available for temperate and equatorial populations than cold-climate ones (Ocobock, 2023). Biocultural adaptations (i.e., body size and shape, brown adipose tissue, subcutaneous fat, fire, clothing, etc.) could have helped some populations buffer thermoregulation costs (Ocobock, Lacy, et al., 2021; Urlacher, 2023). However, the effect of those on the TEE of extinct hominins and the differences between species remains a challenge that may be approached with mathematical modeling in the future. While our study focuses on physiological and methodological constraints, these challenges simultaneously highlight critical opportunities for investigating population-level metabolic adaptations and their evolutionary consequences.

The impact of the variability in organ sizes among species and the energetic consequences was not considered. Müller et al. (2011) have explored the contribution of different organ masses and metabolic rates to the interindividual variability of the RMR. Among the organs with high metabolic rates (Müller et al., 2018), the brain is the only one that has been accurately estimated for past hominins (Neubauer et al., 2018; Wu et al., 2022). Using brain-specific metabolic rate (Elia, 1992), we estimated that *H. neanderthalensis* (~1,500 cm^3 of brain size) would have needed 0.5 MJ/day more per day than *H. erectus* with a brain size of ~1,000 cm^3. However, it is unknown if there were differences in the size of other organs that would affect the RMR of fossil hominins. Importantly, our database included only adult individuals, and organ masses have a greater contribution to RMR for immature individuals (Müller et al., 2018). Furthermore, the proportion of variance accounted for in RMR improves only marginally by the inclusion of organ masses and metabolic rates to prediction equations based on body size, and especially, body composition (Müller et al., 2011). Taken together, the knowledge of the mass of other vital organs would seem unlikely to substantially change our estimation of TEE of past hominids.

The impact of different body proportions on locomotion economy (Aiello & Wells, 2002; Froehle et al., 2013; Steudel-Numbers, 2006) and TEE was not addressed in the present study. However, others have found no significant differences among some species (Vidal-Cordasco et al., 2021). Furthermore, accumulated error in the estimation of sex, BM, and height in fossil hominins likely affected the accuracy of the TEE predictions. Determining these variables from the fossil record is challenging due to the varying preservation of the remains. New studies may yield different findings on hominins' sex, BM, height, and age at death compared to the data presented in SOM 1. However, our data will allow others to refine the results as methods for reconstructing hominin biology continue to advance. In addition, the error of estimation of the predictive equations must be considered (Prado-Nóvoa et al., 2024). We used the averaged TEE of each species to interpret our findings, but we are aware that nonlinear patterns and multidirectional trajectories of body size evolution provide a richer understanding of human phenotypic plasticity and adaptation (Antón & Kuzawa, 2017; Will et al., 2017). Future studies will be necessary to address these knowledge gaps.

The limitations of using modern human equations to predict extinct hominins' TEE must be acknowledged. Phylogenetic differences across genera and species can affect metabolism (Hogg et al., 2020). However, our analyses were restricted to individuals of the *Homo* genus and we utilized equations developed with current *Homo sapiens* populations with the exception of Leonard and Roberton's (1997) model. To the best of our knowledge, two other equations are available in the literature to predict primates' TEE with body mass. One is based on a varied sample of other primates and humans (Pontzer et al., 2014). The other one includes individuals of the *Pan* genus to predict the RMR (Pontzer et al., 2016a) where a PAL could be applied to obtain TEE. Nonetheless, the limitation of phylogenetic differences affecting hominins metabolism would not be overcome by using equations combining multiple genera (i.e., *Pan, Pongo, Papio, Eulemur, Macaca,* etc. in Pontzer et al., 2014) or derived from a single non-human genus (i.e. *Pan* in Pontzer et al., 2016a). As an exception, Leonard and Robertson's (1997) model was used here for comparison with previous studies (Churchill, 2006). There are significant differences in body composition, energy allocation, constraints, and activity levels between humans and other primates (Pontzer, 2015b; Yegian et al., 2024), while similar data on extinct hominins are not available. Extinct species may have had different constraints on TEE and metabolic ceilings. The latter may allow for greater physical activity (Pontzer, 2015a; Yegian et al., 2024), though such activity levels may not have been necessary for a hunter-gatherer lifestyle. We considered using equations based on modern human groups the most straightforward approach due to the lack of detailed data on intraspecies metabolic differences. Although the reliability of these estimates may be uncertain, estimating extinct hominins' TEE is essential for understanding their adaptations, behaviors, and interactions with their environment (Froehle et al., 2013; Leonard, 2018). This knowledge allows us to explore metabolic evolution and offers a valuable context for comparing extinct species with modern humans and non-human primates. Despite the uncertainties, these estimations drive scientific progress by identifying gaps in knowledge and promoting the development of more accurate methods (Yegian et al., 2024).

Early *Homo* species may have had lower energy requirements than predicted here due to a different relationship between TEE and BM compared to later hominins. Models based on other primates produce lower TEE estimates for our sample (see Leonard and Robertson model in Tables 3 and 4). Nevertheless, our analysis would still support the idea of metabolic acceleration in *Homo* compared to other apes (Pontzer et al., 2016a; Yegian et al., 2024) even if early hominins had TEEs that were intermediate between the values predicted here and those of extant apes. This would also align with a gradual increase in energy expenditure associated with body mass evolution up to the Mid-Pleistocene. The possibility that early hominins had lower TEEs than predicted here underscores the need to revise expectations for their PALs and overall energy expenditure.

Collectively, these limitations frame essential research priorities for understanding hominin metabolic evolution. Future studies building on our work could particularly benefit from: (1) integrating population-scale analyses of metabolic variation with cultural/ecological transformations, (2) developing frameworks to connect individual energetic estimates with demographic patterns, and (3) applying comparative approaches across *Homo* species to identify evolutionary thresholds in energetics across *Homo* species. Our findings provide a starting point for these broader investigations of how metabolic shifts shaped hominin lifeways and evolutionary trajectories.

5. Conclusion

In conclusion, our paper advances three new and important ideas. First, we challenge the assumption that extinct hominins engaged in consistently high levels of physical activity, as has been traditionally argued. Our analyses suggest that lower activity levels were more typical, a perspective that builds on Lieberman's (2015) earlier work, but has yet to be fully integrated into evolutionary studies. Our study extends previous work (Aiello & Wells, 2002; Churchill, 2006; Leonard & Robertson, 1997; Snodgrass & Leonard, 2009) by applying recent advances in our understanding of human metabolism to extinct *Homo* species. Second, we propose that metabolic acceleration and deceleration occurred throughout human evolution, driven not only by body size changes but also by technological advancements and social developments. This introduces a novel view of how these factors shaped human biology and offers new avenues for research. Future research will benefit from integrating metabolic reconstructions with archaeological and paleodemographic data in order to formally test the shifts proposed here. Lastly, while body size evolution is critical to our analysis, we argue that TEE estimations provide a more comprehensive understanding of metabolic changes, particularly regarding the role of exosomatic energy sources in human evolution. This study's large-scale analysis of over 100 extinct hominins improves our understanding of the interactions between metabolism, environment, and behavior. It offers insights into hominin adaptation and survival strategies. The findings also help model energetic dynamics in other species and explore new hypotheses on species competition and evolutionary success.

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No potential competing interest was reported by the authors.

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Figure captions

Figure 1. Box and whisker plot of the estimated TEE using Vinken et al. (1999) equation for each species. No significant differences among species were detected (ANOVA test $p>0.05$).

Figure 2. Box and whisker plot of the estimated TEE by sex using Vinken et al. (1999) equation for each species. Asterisks (*) indicate significant differences between sexes (t-test, $p<0.01$).

Figure 3. Total energy expenditure (TEE), in MJ/day estimated according to body composition and compared to Vinken et al. (1999) equation (purple stars: average; brackets: standard deviation). Triangles indicated estimations of TEE using the Pontzer et al. (2021) equation, based on fat-free mass (FFM), and fat mass (FM). Circles indicated resting metabolic rate (RMR) estimated with the Pontzer et al. (2021) equation, based on FFM and FM, and multiplied by a physical activity level (PAL) of 1.89. Orange indicated TEE assuming the minimum normal percentage of FM (20% for females; 12% for males); yellow indicated TEE assuming the maximum normal percentage of FM (30% females; 20% males) for current populations according to FAO/WHO/UNU (2004).

Table captions

Table 1. Body mass (BM), physical activity levels (PAL), total energy expenditure (TEE), and body fat percentage (BF%) for different societies with subsistence economies and comparison with western populations (adults). BM (kg) averaged for both sexes from: [a] Kirchengast (1998), [b] Walker et al. (2006), [c] Leonard et al. (1995), [d] Leonard et al. (1996), [e] Yamauchi et al. (2001), [f] Hildes and Schaefer (1973), [g] Christensen et al. (2012). If not specified, BM was obtained from the same reference as PAL, TEE, and BF%. Both sexes' averages (♀&♂) for PAL and TEE are calculated from the available data in this table. See Gurven et al. (2013) Table 2 for methods to obtain PAL: β factorial method, £ DLW, ¥ Heart Rate Monitor, ∞ Heart Rate Monitor + accelerometry. When available, primary sources and sample sizes for PAL, TEE and BF% are reported, otherwise, Gurven et al., (2013) was used as reference. TEE and BF% data exclusively from DLW measurements.

The overweight and obese individuals (according to BMI) in the Yakut population (Snodgrass et al., 2006) were not considered to calculate the average BF% of this population. Females= ♀; males= ♂.

Table 2. Average body mass (BM) and height of the hominins (adults) used for analysis. Females= ♀; males= ♂. Extracted from Will et al. (2017).

Table 3. Estimated TEE in MJ/day (mean ± standard deviation) for past adult hominins (n=87) using different predictive equations based on body mass. Bold values indicate no statistical difference with the TEE predicted using the Vinken et al. (1999) model (Bonferroni post hoc test, p-value>0.05). *H. antecessor* TEE could not be compared between predictive equations because only one individual is available. No significant differences in TEE among species were detected (ANOVA test p-value>0.05). FAO= FAO/WHO/UNU (2004); Leonard= Leonard and Robertson (1997); Pontzer= Pontzer et al. (2021); Vinken= Vinken et al. (1999).

Table 4. Average difference in MJ/day from subsistence economies' TEE (11.4 MJ/day) using different predictive equations based on body mass. Positive results indicate overestimation while negative results indicate an underestimation. FAO= FAO/WHO/UNU (2004); Leonard= Leonard and Robertson (1997); Pontzer= Pontzer et al. (2021); Vinken= Vinken et al. (1999).

Table 5. Estimated TEE in MJ/day (mean ± standard deviation) by sex for past adult hominins using different predictive equations based on body mass. Differences between sexes were only analyzed for the Vinken et al. (1999) model. Asterisks (*) indicate significant differences (t-test, p<0.01). Females= ♀; males= ♂. FAO= FAO/WHO/UNU (2004); Leonard= Leonard & Robertson (1997); Pontzer= Pontzer et al. (2021); Vinken= Vinken et al. (1999).

Table 6. Total energy expenditure (TEE), in MJ/day estimated according to body composition and compared to Vinken et al. (1999) equation (TEE Vinken). TEE Pontzer= Pontzer et al. (2021) equation, based on fat-free mass and fat mass. Resting metabolic rate (RMR) Pontzer * 1.89= Pontzer et al. (2021) equation for RMR, based on fat-free mass and fat mass, and multiplied by a physical activity level of 1.89. ♀= females; ♂= males. Percentages of Fat Mass (FM %) represent the normal minimum (20% for females; 12% for males) and maximum (30% females; 20% males) ranges for current populations according to FAO/WHO/UNU (2004).

Raw info

	A	B	C	D	E
1	**Prado Nóvoa et al. Slow it down: evolution of human metabolism over two million years.**				
2	**Specimen**	**Sex**	**Chronology (in Mya)**	**Taxonomic group broad**	**Taxonomic group narrow**
3	Fanciulli 4	M	0.011	Late Pleist *H. sapiens*	UP modern humans
4	Fanciulli 5	F	0.011	Late Pleist *H. sapiens*	UP modern humans
5	Chancelade 1	M	0.012	Late Pleist *H. sapiens*	UP modern humans
6	Oberkassel 1	M	0.012	Late Pleist *H. sapiens*	UP modern humans
7	Oberkassel 2	F	0.012	Late Pleist *H. sapiens*	UP modern humans
8	Cap Blanc 1	F	0.014	Late Pleist *H. sapiens*	UP modern humans
9	Gough's Cave 1	M	0.0147	Late Pleist *H. sapiens*	UP modern humans
10	Mirón 1	F	0.0155	Late Pleist *H. sapiens*	UP modern humans
11	Minatogawa 1	M	0.017	Late Pleist *H. sapiens*	UP modern humans
12	Minatogawa 2	F	0.017	Late Pleist *H. sapiens*	UP modern humans
13	Minatogawa 3	F	0.017	Late Pleist *H. sapiens*	UP modern humans
14	Minatogawa 4	F	0.017	Late Pleist *H. sapiens*	UP modern humans
15	Zhoukoudian-UC 105	M[b]	0.018	Late Pleist *H. sapiens*	UP modern humans
16	Zhoukoudian-UC 117	F[b]	0.018	Late Pleist *H. sapiens*	UP modern humans
17	Ohalo 2	M	0.019	Late Pleist *H. sapiens*	UP modern humans
18	Paglicci 25	F	0.023	Late Pleist *H. sapiens*	UP modern humans
19	Veneri 1	M	0.024	Late Pleist *H. sapiens*	UP modern humans
20	Veneri 2	F	0.024	Late Pleist *H. sapiens*	UP modern humans
21	Barma Grande 2	M	0.0245	Late Pleist *H. sapiens*	UP modern humans
22	Caviglione 1	F	0.025	Late Pleist *H. sapiens*	UP modern humans
23	Předmostí 1	F	0.0255	Late Pleist *H. sapiens*	UP modern humans
24	Předmostí 3	M	0.0255	Late Pleist *H. sapiens*	UP modern humans
25	Předmostí 4	F	0.0255	Late Pleist *H. sapiens*	UP modern humans
26	Předmostí 9	M	0.0255	Late Pleist *H. sapiens*	UP modern humans
27	Předmostí 10	F	0.0255	Late Pleist *H. sapiens*	UP modern humans
28	Předmostí 14	M	0.0255	Late Pleist *H. sapiens*	UP modern humans
29	Dolní Věstonice 3	F	0.026	Late Pleist *H. sapiens*	UP modern humans
30	Dolní Věstonice 13	M	0.026	Late Pleist *H. sapiens*	UP modern humans
31	Dolní Věstonice 14	M	0.026	Late Pleist *H. sapiens*	UP modern humans
32	Dolní Věstonice 15	M	0.026	Late Pleist *H. sapiens*	UP modern humans
33	Dolní Věstonice 16	M	0.026	Late Pleist *H. sapiens*	UP modern humans
34	Sunghir 1	M	0.0275	Late Pleist *H. sapiens*	UP modern humans
35	Cro-magnon 1 (CM-1)	M	0.028	Late Pleist *H. sapiens*	UP modern humans
36	Cro-magnon 4314	M	0.028	Late Pleist *H. sapiens*	UP modern humans
37	Cro-magnon 4315	M	0.028	Late Pleist *H. sapiens*	UP modern humans
38	Cro-magnon 4337	F	0.028	Late Pleist *H. sapiens*	UP modern humans
39	Paviland 1	M	0.028	Late Pleist *H. sapiens*	UP modern humans
40	Abri Pataud 1	F	0.031	Late Pleist *H. sapiens*	UP modern humans
41	Mladeč 21	F	0.031	Late Pleist *H. sapiens*	UP modern humans
42	Spy 2	M	0.033	Neanderthals	*H. neanderthalensis*
43	Neandertal 1 (Feldhofer)	M	0.04	Neanderthals	*H. neanderthalensis*
44	Sima de las Palomas 96	F	0.045	Neanderthals	*H. neanderthalensis*
45	La Ferrassie 1	M	0.047	Neanderthals	*H. neanderthalensis*
46	La Ferrassie 2	F	0.047	Neanderthals	*H. neanderthalensis*
47	Shanidar 1	M	0.0475	Neanderthals	*H. neanderthalensis*
48	Shanidar 3	M	0.0475	Neanderthals	*H. neanderthalensis*
49	Shanidar 4	M	0.0475	Neanderthals	*H. neanderthalensis*
50	Shanidar 5	M	0.0475	Neanderthals	*H. neanderthalensis*
51	La Chapelle-aux-Saints 1	M	0.051	Neanderthals	*H. neanderthalensis*
52	Amud 1	M	0.06	Neanderthals	*H. neanderthalensis*
53	Kebara 2	M	0.06	Neanderthals	*H. neanderthalensis*
54	Regourdou 1	M	0.066	Neanderthals	*H. neanderthalensis*
55	Liujiang 1	F	0.07	Late Pleist *H. sapiens*	MP *Homo sapiens*
56	Qafzeh 3	F	0.091	Late Pleist *H. sapiens*	MP *Homo sapiens*
57	Qafzeh 8	M	0.091	Late Pleist *H. sapiens*	MP *Homo sapiens*
58	Qafzeh 9	F[c]	0.091	Late Pleist *H. sapiens*	MP *Homo sapiens*
59	Qafzeh 9	M[d]	0.091	Late Pleist *H. sapiens*	MP *Homo sapiens*
60	Kiik-Koba 1	M	0.10	Neanderthals	*H. neanderthalensis*
61	Skhul 4	M	0.119	Late Pleist *H. sapiens*	MP *Homo sapiens*
62	Skhul 5	M	0.119	Late Pleist *H. sapiens*	MP *Homo sapiens*
63	Skhul 6	M	0.119	Late Pleist *H. sapiens*	MP *Homo sapiens*
64	Skhul 7	F	0.119	Late Pleist *H. sapiens*	MP *Homo sapiens*
65	Skhul 9	M	0.119	Late Pleist *H. sapiens*	MP *Homo sapiens*
66	Krapina foot A	F	0.13	Neanderthals	*H. neanderthalensis*
67	Krapina 208	F[e]	0.13	Neanderthals	*H. neanderthalensis*

Raw info

	A	B	C	D	E
68	Kaprina 214	F[e]	0.13	Neanderthals	*H. neanderthalensis*
69	Krapina 236	F	0.13	Neanderthals	*H. neanderthalensis*
70	Krapina 237	M	0.13	Neanderthals	*H. neanderthalensis*
71	Tabun C1	F	0.17	Neanderthals	*H. neanderthalensis*
72	Omo Kibish 1	F	0.195	Late Pleist *H. sapiens*	MP *Homo sapiens*
73	Jinniushan 1	F	0.2	Early Mid-Pleistocene *Homo*	*Homo erectus sl*
74	Broken Hill E689 (Femur)	M[f]	0.4	Early Mid-Pleistocene *Homo*	Mid-Pleistocene *Homo*
75	Broken Hill E907 (Femur)	M[f]	0.4	Early Mid-Pleistocene *Homo*	Mid-Pleistocene *Homo*
76	AT-800 (coxal)	M	0.43	SH hominins	Mid-Pleistocene *Homo*
77	AT-835+AT-2501 (coxal)	M	0.43	SH hominins	Mid-Pleistocene *Homo*
78	AT-860	F	0.43	SH hominins	Mid-Pleistocene *Homo*
79	AT-1004 (coxal)	F	0.43	SH hominins	Mid-Pleistocene *Homo*
80	AT-1930	F	0.43	SH hominins	Mid-Pleistocene *Homo*
81	AT-2350 (coxal)	M	0.43	SH hominins	Mid-Pleistocene *Homo*
82	AT-2803	M	0.43	SH hominins	Mid-Pleistocene *Homo*
83	AT-3132	F	0.43	SH hominins	Mid-Pleistocene *Homo*
84	AT-4425	F	0.43	SH hominins	Mid-Pleistocene *Homo*
85	SH Pelvis 1	M	0.43	SH hominins	Mid-Pleistocene *Homo*
86	SH Coxal 1 (Coxal)	F	0.43	SH hominins	Mid-Pleistocene *Homo*
87	SH Femur X	M	0.43	SH hominins	Mid-Pleistocene *Homo*
88	F-X + Pelvis 1	M	0.43	SH hominins	Mid-Pleistocene *Homo*
89	SH Femur XI	F	0.43	SH hominins	Mid-Pleistocene *Homo*
90	F-XII	F[g]	0.43	SH hominins	Mid-Pleistocene *Homo*
91	F-XIII	F[g]	0.43	SH hominins	Mid-Pleistocene *Homo*
92	SH Femur XII/XIII	M	0.43	SH hominins	Mid-Pleistocene *Homo*
93	SH Femur XVI	F	0.43	SH hominins	Mid-Pleistocene *Homo*
94	SH foot association 1	M	0.43	SH hominins	Mid-Pleistocene *Homo*
95	SH foot association 2	F	0.43	SH hominins	Mid-Pleistocene *Homo*
96	SH foot association 5	M	0.43	SH hominins	Mid-Pleistocene *Homo*
97	SH foot association 8	M	0.43	SH hominins	Mid-Pleistocene *Homo*
98	SH foot association 9	F	0.43	SH hominins	Mid-Pleistocene *Homo*
99	Arago 44	M[i]	0.475	Early Mid-Pleistocene *Homo*	Mid-Pleistocene *Homo*
100	Boxgrove	M	0.5	Early Mid-Pleistocene *Homo*	Mid-Pleistocene *Homo*
101	OH 28	F	0.7	Early Mid-Pleistocene *Homo*	*Homo erectus sl*
102	Trinil I	M	0.9	Early Mid-Pleistocene *Homo*	*Homo erectus sl*
103	TD6 Hominin 10	M	0.925	Early Mid-Pleistocene *Homo*	*Homo antecessor*
104	OH 34	F[i]	0.975	Early Mid-Pleistocene *Homo*	*Homo erectus sl*
105	BSN49/P27 (Gona pelvis)	F	1.15	Early *Homo*	*Homo erectus sl*
106	KNM-WT 15000 (adult)	M	1.47	Early *Homo*	*Homo erectus sl*
107	KNM-ER 803	F[j]	1.5	Early *Homo*	*Homo erectus sl*
108	KNM-ER 736	M[j]	1.58	Early *Homo*	*Homo erectus sl*
109	KNM-ER 737	F[j]	1.6	Early *Homo*	*Homo erectus sl*
110	KNM-ER 1808	F[k]	1.6	Early *Homo*	*Homo erectus sl*
111	KNM-ER 5428	M[l]	1.65	Early *Homo*	*Homo erectus sl*
112	D2600 (D4167)	M[m]	1.8	Early *Homo*	*Homo erectus sl*
113	KNM-ER 1481	M[n]	1.95	Early *Homo*	*Homo erectus sl*
114	KNM-ER 1472	M[j]	2	Early *Homo*	*Homo erectus sl*

Raw info

	F	G	H	I
1				
2	**Body mass estimate (kg) [a]**	**Stature estimate (cm) [a]**	**Estimated age at death according to the literature**	**Estimated age at death used for analyses**
3	82.5		Older adolescent; adult	20.00
4	52.1		Older adolescent; adult	20.00
5	67.4	159.8	35-40	37.50
6	75.1	174.8	50-60	55.00
7	58.8	146.5	20-25	22.50
8	59.4	160.8	20 ~	20.00
9	70.1	168.0	18-23	20.50
10	56.9	160.7	35-40	37.50
11	63.3	152.9	25-30	27.50
12	48.6	144.8	Not available (na)	20.00
13	50.8	149.3	na	20.00
14	47.4	147.7	na	20.00
15	71.8		na	20.00
16	59.0		na	20.00
17	74.9	175.0	35-40	37.50
18	61.7	170.4	18-20; 18-25	21.50
19	77.1	177.1	30-35	32.50
20	74.2	173.2	30-35	32.50
21	82.3	188.8	30-35	32.50
22	68.1	175.1	Adult	20.00
23	56.5	153.7	20-25	22.50
24	70.1	182.0	35-40	37.50
25	70.5	168.2	35-40	37.50
26	58.8	169.9	20-25	22.50
27	71.9	163.4	20-25	22.50
28	68.5	173.6	35+	36.00
29	55.8	163.4	36-45; 35; 38-43	40.00
30	71.2	171.6	17-19; 21-25; 17-23	21.00
31	79.4	185.0	16-17; Late 20s; 17-23	22.00
32	69.8	160.1	20; Early 30s; 17-23	23.50
33	78.0	174.2	40+; 50s; 40-50	45.00
34	78.9	183.6	35-45; 55-65	50.00
35	70.3	172.1	Older adult; +50	51.00
36	70.1		Older adult; +50	51.00
37	73.5		Adult	20.00
38	81.1	170.2	Adult	20.00
39	74.0	176.5	20-29; 25 ~	24.50
40	69.7	162.2	20-29	24.50
41	65.6		Adult	20.00
42	82.6	158.6	16-30	23.00
43	81.4	165.6	Adult	20.00
44	61.0	149.2	16-20	20.00
45	90.5	171.6	40 ~	40.00
46	67.8	148.7	25-30	27.50
47	67.8	167.2	40-50	42.50
48	72.7	166.4	41.0	41.00
49	74.6	162.5	30-40	35.00
50	71.2	163.6	40+	41.00
51	81.7	162.5	50 ~	50.00
52	72.1	175.7	25-30	27.50
53	72.4	172.0	32.0	32.00
54	64.4	162.3	23-30	26.50
55	42.7		late 30s	38.00
56	46.7	164.8	Adult; older adult	35.00
57	59.9	191.4	Adult; older adult	35.00
58	64.4	172.5	16-21; 18.5-20.5	20.00
59	64.4	172.5	16-21; 18.5-20.5	20.00
60	80.2	162.7	40 ~	40.00
61	72.4	182.0	40-50	45.00
62	76.9	181.6	30-40	35.00
63	69.0	177.9	28.0	28.00
64	57.9	158.5	na	20.00
65	74.0		na	20.00
66	59.2	163.2	na	20.00
67	67.4		na	20.00

Raw info

	F	G	H	I
68	63.7		Young adult	20.00
69	59.7	160.0	na	20.00
70	77.5	171.1	na	20.00
71	54.2	153.1	30 ~	30.00
72	54.1	163.3	Young adult	20.00
73	77.4	168.8	na	20.00
74	75.8		na	20.00
75	82.6		na	20.00
76	75.8		Fully adult	20.00
77	77.8		Fully adult	20.00
78	62.5	161.0	Fully adult	20.00
79	66.2		Fully adult	20.00
80	66.1	162.8	Fully adult	20.00
81	75.8		Fully adult	20.00
82	80.3	174.0	Fully adult	20.00
83	75.6	164.3	Fully adult	20.00
84	72.1	163.6	Fully adult	20.00
85	78.7		> 45	46.00
86	56.9		Fully adult	20.00
87	83.3	170.0	>45 if associated to Pelvis I	46.00
88	96,93[g]	170[h]	> 45	46.00
89	58.3		Fully adult	20.00
90	75.4		Adults	20.00
91	73.9		Adults	20.00
92	73.8	167.8	>45 if associated to Pelvis I	46.00
93	56.9		Adult	20.00
94	73.0	173.7	Fully adult	20.00
95	57.6	161.3	Fully adult	20.00
96	90.7	175.3	Fully adult	20.00
97	65.7	173.7	Fully adult	20.00
98	62.6	159.8	Fully adult	20.00
99	79.6		na	20.00
100	82.8	175.3	Late 40s	48.00
101	62.2	164.8	Adult; +21	22.00
102	51.7	171.1	na	20.00
103	76.0	174.5	Adult	20.00
104	55.3	160.5	na	20.00
105	56.5		na	20.00
106	81.0	178.0	Adult projected according B	20.00
107	69.0	156.7	Adult	20.00
108	80.0	172.6	na	20.00
109	78.0	167.41	na	20.00
110	79	173.19	Adult	20.00
111	61.0	162.65	Adult	20.00
112	53	146.69	Mature/old adult	35.00
113	61	152.47	na	20.00
114	53	153.73	Adult	20.00

Raw info

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1	
2	**Source of age at death**
3	French and Nowell, 2022; Manolis and Mallegni, 1996
4	French and Nowell, 2022; Manolis and Mallegni, 1996
5	Friedl et al., 2016
6	Friedl et al., 2016
7	Friedl et al., 2016
8	Friedl et al., 2016
9	Friedl et al., 2016
10	Carretero et al., 2015
11	Friedl et al., 2016
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17	Friedl et al., 2016
18	Friedl et al., 2016; French and Nowell, 2022
19	French and Nowell, 2022
20	French and Nowell, 2022
21	French and Nowell, 2022
22	Manolis and Mallegni, 1996
23	French and Nowell, 2022
24	French and Nowell, 2022
25	French and Nowell, 2022
26	French and Nowell, 2022
27	French and Nowell, 2022
28	French and Nowell, 2022
29	French and Nowell, 2022; Trinkaus and Svodoba, 2006; Friedl et al., 2016.
30	French and Nowell, 2022; Trinkaus and Svodoba, 2006; Friedl et al., 2016.
31	French and Nowell, 2022; Trinkaus and Svodoba, 2006; Friedl et al., 2016.
32	French and Nowell, 2022; Trinkaus and Svodoba, 2006; Friedl et al., 2016.
33	French and Nowell, 2022; Trinkaus and Svodoba, 2006; Friedl et al., 2016.
34	French and Nowell, 2022; Trinkaus and Svodoba, 2006; Friedl et al., 2016.
35	French and Nowell, 2022; Friedl et al., 2016
36	Thibeault and Villotte, 2018
37	Thibeault and Villotte, 2018
38	Thibeault and Villotte, 2018
39	French and Nowell, 2022; Friedl et al., 2016
40	French and Nowell, 2022
41	Teschler-Nicola et al., 2006
42	Friedl et al., 2016
43	Friedl et al., 2016
44	Friedl et al., 2016
45	Friedl et al., 2016
46	Friedl et al., 2016
47	Trinkaus and Villotte, 2017
48	Trinkaus and Thompson, 1987
49	Friedl et al., 2016
50	Friedl et al., 2016
51	Friedl et al., 2016
52	Friedl et al., 2016
53	Karasik et al., 1998
54	Volpato et al., 2012
55	Brown, 1999
56	Tillier, 2021; Tillier et al., 2004
57	Tillier, 2021; Tillier et al., 2004
58	Friedl et al., 2016; Coutinho-Nogueira et al., 2021
59	Friedl et al., 2016; Coutinho-Nogueira et al., 2021
60	Trinkaus et al., 2008
61	Friedl et al., 2016
62	Friedl et al., 2016
63	Friedl et al., 2016
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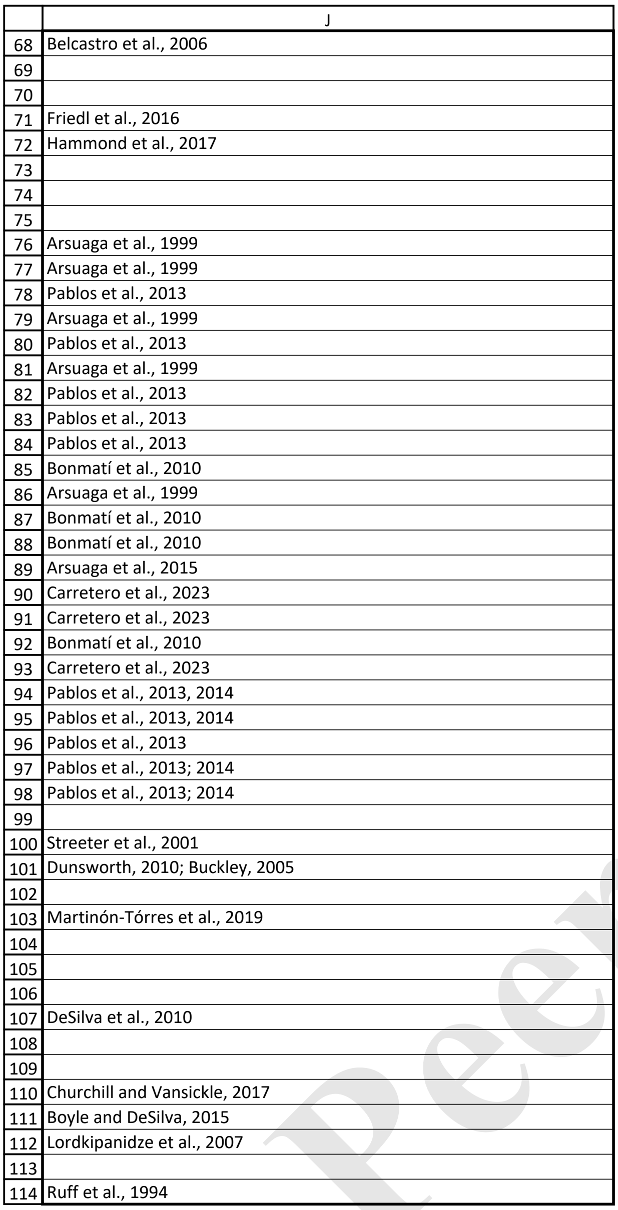
Raw info



	J
68	Belcastro et al., 2006
69	
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71	Friedl et al., 2016
72	Hammond et al., 2017
73	
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76	Arsuaga et al., 1999
77	Arsuaga et al., 1999
78	Pablos et al., 2013
79	Arsuaga et al., 1999
80	Pablos et al., 2013
81	Arsuaga et al., 1999
82	Pablos et al., 2013
83	Pablos et al., 2013
84	Pablos et al., 2013
85	Bonmatí et al., 2010
86	Arsuaga et al., 1999
87	Bonmatí et al., 2010
88	Bonmatí et al., 2010
89	Arsuaga et al., 2015
90	Carretero et al., 2023
91	Carretero et al., 2023
92	Bonmatí et al., 2010
93	Carretero et al., 2023
94	Pablos et al., 2013, 2014
95	Pablos et al., 2013, 2014
96	Pablos et al., 2013
97	Pablos et al., 2013; 2014
98	Pablos et al., 2013; 2014
99	
100	Streeter et al., 2001
101	Dunsworth, 2010; Buckley, 2005
102	
103	Martinón-Tórres et al., 2019
104	
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107	DeSilva et al., 2010
108	
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110	Churchill and Vansickle, 2017
111	Boyle and DeSilva, 2015
112	Lordkipanidze et al., 2007
113	
114	Ruff et al., 1994

Raw info

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2	Other notes
3	[a] Body mass and stature from Will et al. 2017 except when referred otherwise. See details in Will et al. 2017 supplementary information for sources of estimation
4	[b]Ruff et al., 2022
5	[c]Friedl et al., 2016
6	[d]Coutinho-Nogueira et al., 2021
7	[e]Trinkaus, 1980
8	[f]Kennedy, 1984
9	[g]Carretero et al., 2023
10	[h]Carretero et al., 2012
11	[i]Robson and Wood, 2008
12	[j]McHenry, 1991
13	[k]Churchill and Vansickle, 2017
14	[l]Cunningham et al., 2019; Boyle and DeSilva, 2015
15	[m]Rightmire et al., 2018
16	[n]Kennedy, 1983; McHenry, 1991
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TEE estimations

	A	B	C	D	E	F	G	H
1	**Prado Nóvoa et al. Slow it down: evolution of human metabolism over two million years.**							
2	Specimen	ID n	Sex	Taxonomic group narrow	Body mass estimate (kg)	Stature estimate (cm)	Height (m)	Age at death
3	Fanciulli 4	1	M	UP modern humans	82.5			20.0
4	Fanciulli 5	2	F	UP modern humans	52.1			20.0
5	Chancelade 1	3	M	UP modern humans	67.4	159.8	1.60	37.5
6	Oberkassel 1	4	M	UP modern humans	75.1	174.8	1.75	55.0
7	Oberkassel 2	5	F	UP modern humans	58.8	146.5	1.47	22.5
8	Cap Blanc 1	6	F	UP modern humans	59.4	160.8	1.61	20.0
9	Gough's Cave 1	7	M	UP modern humans	70.1	168.0	1.68	20.5
10	Mirón 1	8	F	UP modern humans	56.9	160.7	1.61	37.5
11	Minatogawa 1	9	M	UP modern humans	63.3	152.9	1.53	27.5
12	Minatogawa 2	10	F	UP modern humans	48.6	144.8	1.45	20.0
13	Minatogawa 3	11	F	UP modern humans	50.8	149.3	1.49	20.0
14	Minatogawa 4	12	F	UP modern humans	47.4	147.7	1.48	20.0
15	Zhoukoudian-UC 105	13	M	UP modern humans	71.8			20.0
16	Zhoukoudian-UC 117	14	F	UP modern humans	59.0			20.0
17	Ohalo 2	15	M	UP modern humans	74.9	175.0	1.75	37.5
18	Paglicci 25	16	F	UP modern humans	61.7	170.4	1.70	21.5
19	Veneri 1	17	M	UP modern humans	77.1	177.1	1.77	32.5
20	Veneri 2	18	F	UP modern humans	74.2	173.2	1.73	32.5
21	Barma Grande 2	19	M	UP modern humans	82.3	188.8	1.89	32.5
22	Caviglione 1	20	F	UP modern humans	68.1	175.1	1.75	20.0
23	Předmostí 1	21	F	UP modern humans	56.5	153.7	1.54	22.5
24	Předmostí 3	22	M	UP modern humans	70.1	182.0	1.82	37.5
25	Předmostí 4	23	F	UP modern humans	70.5	168.2	1.68	37.5
26	Předmostí 9	24	M	UP modern humans	58.8	169.9	1.70	22.5
27	Předmostí 10	25	F	UP modern humans	71.9	163.4	1.63	22.5
28	Předmostí 14	26	M	UP modern humans	68.5	173.6	1.74	36.0
29	Dolní Věstonice 3	27	F	UP modern humans	55.8	163.4	1.63	40.0
30	Dolní Věstonice 13	28	M	UP modern humans	71.2	171.6	1.72	21.0
31	Dolní Věstonice 14	29	M	UP modern humans	79.4	185.0	1.85	22.0
32	Dolní Věstonice 15	30	M	UP modern humans	69.8	160.1	1.60	23.5
33	Dolní Věstonice 16	31	M	UP modern humans	78.0	174.2	1.74	45.0
34	Sunghir 1	32	M	UP modern humans	78.9	183.6	1.84	50.0
35	Cro-magnon 1 (CM-1)	33	M	UP modern humans	70.3	172.1	1.72	51.0
36	Cro-magnon 4314	34	M	UP modern humans	70.1			51.0
37	Cro-magnon 4315	35	M	UP modern humans	73.5			20.0
38	Cro-magnon 4337	36	F	UP modern humans	81.1	170.2	1.70	20.0
39	Paviland 1	37	M	UP modern humans	74.0	176.5	1.77	24.5
40	Abri Pataud 1	38	F	UP modern humans	69.7	162.2	1.62	24.5
41	Mladeč 21	39	F	UP modern humans	65.6			20.0
42	Spy 2	40	M	H. neanderthalensis	82.6	158.6	1.59	23.0
43	Neandertal 1 (Feldhofer)	41	M	H. neanderthalensis	81.4	165.6	1.66	20.0
44	Sima de las Palomas 96	42	F	H. neanderthalensis	61.0	149.2	1.49	20.0
45	La Ferrassie 1	43	M	H. neanderthalensis	90.5	171.6	1.72	40.0
46	La Ferrassie 2	44	F	H. neanderthalensis	67.8	148.7	1.49	27.5
47	Shanidar 1	45	M	H. neanderthalensis	67.8	167.2	1.67	42.5
48	Shanidar 3	46	M	H. neanderthalensis	72.7	166.4	1.66	41.0
49	Shanidar 4	47	M	H. neanderthalensis	74.6	162.5	1.63	35.0
50	Shanidar 5	48	M	H. neanderthalensis	71.2	163.6	1.64	41.0
51	La Chapelle-aux-Saints 1	49	M	H. neanderthalensis	81.7	162.5	1.63	50.0
52	Amud 1	50	M	H. neanderthalensis	72.1	175.7	1.76	27.5
53	Kebara 2	51	M	H. neanderthalensis	72.4	172.0	1.72	32.0
54	Regourdou 1	52	M	H. neanderthalensis	64.4	162.3	1.62	26.5
55	Liujiang 1	53	F	MP Homo sapiens	42.7			38.0
56	Qafzeh 3	54	F	MP Homo sapiens	46.7	164.8	1.65	35.0
57	Qafzeh 8	55	M	MP Homo sapiens	59.9	191.4	1.91	35.0
58	Qafzeh 9	56	M	MP Homo sapiens	64.4	172.5	1.73	20.0
59	Qafzeh 9	57	F	MP Homo sapiens	64.4	172.5	1.73	20.0
60	Kiik-Koba 1	58	M	H. neanderthalensis	80.2	162.7	1.63	40.0
61	Skhul 4	59	M	MP Homo sapiens	72.4	182.0	1.82	45.0
62	Skhul 5	60	M	MP Homo sapiens	76.9	181.6	1.82	35.0
63	Skhul 6	61	M	MP Homo sapiens	69.0	177.9	1.78	28.0
64	Skhul 7	62	F	MP Homo sapiens	57.9	158.5	1.59	20.0
65	Skhul 9	63	M	MP Homo sapiens	74.0			20.0
66	Krapina foot A	64	F	H. neanderthalensis	59.2	163.2	1.63	20.0
67	Krapina 208	65	F	H. neanderthalensis	67.4			20.0
68	Kaprina 214	66	F	H. neanderthalensis	63.7			20.0
69	Krapina 236	67	F	H. neanderthalensis	59.7	160.0	1.60	20.0
70	Krapina 237	68	M	H. neanderthalensis	77.5	171.1	1.71	20.0
71	Tabun C1	69	F	H. neanderthalensis	54.2	153.1	1.53	30.0

TEE estimations

	A	B	C	D	E	F	G	H
72	Omo Kibish 1	70	M	MP Homo sapiens	54.1	163.3	1.63	20.0
73	Jinniushan 1	71	F	Homo erectus sl	77.4	168.8	1.69	20.0
74	Broken Hill E689 (Femur)	72	M	Mid-Pleistocene Homo	75.8			20.0
75	Broken Hill E907 (Femur)	73	M	Mid-Pleistocene Homo	82.6			20.0
76	AT-800 (coxal)	74	M	Mid-Pleistocene Homo	75.8			20.0
77	AT-835+AT-2501 (coxal)	75	M	Mid-Pleistocene Homo	77.8			20.0
78	AT-860	76	F	Mid-Pleistocene Homo	62.5	161.0	1.61	20.0
79	AT-1004 (coxal)	77	F	Mid-Pleistocene Homo	66.2			20.0
80	AT-1930	78	F	Mid-Pleistocene Homo	66.1	162.8	1.63	20.0
81	AT-2350 (coxal)	79	M	Mid-Pleistocene Homo	75.8			20.0
82	AT-2803	80	M	Mid-Pleistocene Homo	80.3	174.0	1.74	20.0
83	AT-3132	81	F	Mid-Pleistocene Homo	75.6	164.3	1.64	20.0
84	AT-4425	82	F	Mid-Pleistocene Homo	72.1	163.6	1.64	20.0
85	SH Pelvis 1	83	M	Mid-Pleistocene Homo	78.7			46.0
86	SH Coxal 1 (Coxal)	84	F	Mid-Pleistocene Homo	56.9			20.0
87	SH Femur X	85	M	Mid-Pleistocene Homo	83.3	170.0	1.70	46.0
88	F-X + Pelvis 1	86	M	Mid-Pleistocene Homo	96.9	170.0	1.70	46.0
89	SH Femur XI	87	F	Mid-Pleistocene Homo	58.3			20.0
90	F-XII	88	F	Mid-Pleistocene Homo	75.4			20.0
91	F-XIII	89	F	Mid-Pleistocene Homo	73.9			20.0
92	SH Femur XII/XIII	90	M	Mid-Pleistocene Homo	73.8	167.8	1.68	46.0
93	SH Femur XVI	91	F	Mid-Pleistocene Homo	56.9			20.0
94	SH foot association 1	92	M	Mid-Pleistocene Homo	73.0	173.7	1.74	20.0
95	SH foot association 2	93	F	Mid-Pleistocene Homo	57.6	161.3	1.61	20.0
96	SH foot association 5	94	M	Mid-Pleistocene Homo	90.7	175.3	1.75	20.0
97	SH foot association 8	95	M	Mid-Pleistocene Homo	65.7	173.7	1.74	20.0
98	SH foot association 9	96	F	Mid-Pleistocene Homo	62.6	159.8	1.60	20.0
99	Arago 44	97	M	Mid-Pleistocene Homo	79.6			20.0
100	Boxgrove	98	M	Mid-Pleistocene Homo	82.8	175.3	1.75	48.0
101	OH 28	99	F	Homo erectus sl	62.2	164.8	1.65	22.0
102	Trinil I	100	M	Homo erectus sl	51.7	171.1	1.71	20.0
103	TD6 Hominin 10	101	M	Homo antecessor	76.0	174.5	1.75	20.0
104	OH 34	102	F	Homo erectus sl	55.3	160.5	1.61	20.0
105	BSN49/P27 (Gona pelvis)	103	F	Homo erectus sl	56.5			20.0
106	KNM-WT 15000 (adult)	104	M	Homo erectus sl	81.0	178.0	1.78	20.0
107	KNM-ER 803	105	F	Homo erectus sl	69.0	156.7	1.57	20.0
108	KNM-ER 736	106	M	Homo erectus sl	80.0	172.6	1.73	20.0
109	KNM-ER 737	107	F	Homo erectus sl	78.0	167.4	1.67	20.0
110	KNM-ER 1808	108	F	Homo erectus sl	79.0	173.2	1.73	20.0
111	KNM-ER 5428	109	M	Homo erectus sl	61.0	162.7	1.63	20.0
112	D2600 (D4167)	110	M	Homo erectus sl	53.0	146.7	1.47	35.0
113	KNM-ER 1481	111	M	Homo erectus sl	61.0	152.5	1.52	20.0
114	KNM-ER 1472	112	M	Homo erectus sl	53.0	153.7	1.54	20.0

TEE estimations

	I	J	K	L	M	N	O
1							
2	Vinken TEE (MJ)	Vinken TEE (kcal)	Pontzer TEE (MJ)	Pontzer TEE (kcal)	Leonard TEE (MJ)	Leonard TEE (kcal)	RMR from FAO (MJ)
3			13.5	3230	11.9	2846	8.1
4			8.9	2120	8.3	1977	5.3
5	12.2	2922	12.1	2891	10.1	2424	6.9
6	11.8	2814	12.2	2906	11.1	2641	7.3
7	11.1	2649	9.2	2209	9.1	2174	5.7
8	11.5	2752	9.3	2234	9.2	2194	5.7
9	13.8	3298	12.7	3035	10.5	2501	7.3
10	10.0	2398	8.7	2091	8.9	2121	5.5
11	12.5	2996	12.1	2887	9.7	2307	6.9
12	10.4	2491	8.6	2065	7.8	1869	5.0
13	10.7	2549	8.8	2100	8.1	1938	5.2
14	10.4	2478	8.6	2047	7.7	1834	5.0
15			12.8	3064	10.7	2549	7.4
16			9.3	2227	9.1	2182	5.7
17	13.0	3116	12.6	3007	11.0	2635	7.2
18	11.7	2801	9.5	2260	9.5	2261	5.9
19	13.6	3253	12.9	3072	11.3	2698	7.4
20	12.0	2858	10.0	2388	10.9	2616	6.1
21	14.2	3392	13.2	3153	11.9	2842	7.6
22	12.4	2964	9.9	2368	10.2	2443	6.3
23	11.0	2629	9.1	2173	8.8	2108	5.5
24	12.7	3046	12.3	2933	10.5	2501	7.0
25	11.2	2685	9.6	2302	10.5	2514	5.9
26	12.8	3051	11.9	2847	9.1	2174	6.6
27	12.4	2957	10.1	2413	10.7	2552	6.5
28	12.6	3015	12.2	2917	10.3	2456	6.9
29	9.8	2342	8.6	2058	8.7	2087	5.4
30	13.9	3323	12.8	3049	10.6	2533	7.4
31	14.7	3506	13.3	3170	11.6	2761	7.9
32	13.4	3214	12.6	3011	10.4	2491	7.3
33	12.7	3043	12.6	3012	11.4	2723	7.4
34	12.6	3004	12.5	2996	11.5	2748	7.4
35	11.6	2783	11.9	2856	10.5	2508	7.0
36			11.9	2852	10.5	2501	7.0
37			12.9	3090	10.9	2597	7.5
38	13.4	3199	10.8	2570	11.7	2806	7.1
39	13.9	3330	12.8	3071	10.9	2610	7.6
40	12.0	2876	9.9	2367	10.4	2490	6.4
41			9.7	2329	9.9	2372	6.1
42	14.5	3464	13.4	3214	11.9	2848	8.1
43	14.7	3517	13.4	3214	11.8	2817	8.0
44	11.5	2745	9.5	2259	9.4	2241	5.8
45	14.1	3363	13.5	3235	12.8	3063	8.0
46	11.5	2744	9.7	2320	10.2	2437	6.2
47	12.0	2868	12.0	2868	10.2	2437	6.9
48	12.5	2985	12.4	2953	10.8	2575	7.1
49	13.0	3115	12.6	3018	11.0	2629	7.2
50	12.3	2948	12.3	2930	10.6	2533	7.1
51	12.5	2988	12.7	3038	11.8	2823	7.6
52	13.6	3239	12.7	3024	10.7	2558	7.4
53	13.2	3155	12.6	3002	10.7	2566	7.1
54	12.8	3066	12.2	2911	9.8	2339	7.0
55			7.8	1867	7.1	1688	5.0
56	9.5	2259	8.1	1947	7.6	1814	5.1
57	12.2	2924	11.7	2790	9.2	2208	6.5
58	13.4	3212	12.3	2950	9.8	2339	7.0
59	12.1	2886	9.7	2312	9.8	2339	6.0
60	13.1	3135	12.9	3075	11.6	2783	7.5
61	12.4	2959	12.2	2923	10.7	2565	7.1
62	13.5	3220	12.8	3054	11.3	2692	7.3
63	13.3	3177	12.4	2972	10.3	2469	7.2
64	11.4	2716	9.2	2211	9.0	2150	5.6
65			13.0	3098	10.9	2610	7.6
66	11.5	2755	9.3	2230	9.2	2187	5.7
67			9.9	2357	10.1	2424	6.2
68			9.6	2301	9.7	2320	6.0
69	11.5	2756	9.4	2239	9.2	2203	5.7
70	14.5	3460	13.2	3153	11.3	2709	7.8
71	10.3	2452	8.8	2093	8.5	2040	5.4

TEE estimations

	I	J	K	L	M	N	O
72	12.5	2983	11.7	2789	8.5	2037	6.3
73	13.1	3123	10.5	2512	11.3	2704	6.8
74			13.1	3126	11.1	2660	7.7
75			13.5	3231	11.9	2848	8.1
76			13.1	3126	11.1	2660	7.7
77			13.2	3157	11.4	2717	7.8
78	11.8	2812	9.5	2282	9.6	2284	5.9
79			9.8	2340	10.0	2391	6.1
80	12.1	2887	9.8	2338	10.0	2387	6.1
81			13.1	3126	11.1	2660	7.7
82	14.7	3523	13.4	3196	11.7	2786	8.0
83	12.9	3075	10.4	2485	11.1	2656	6.7
84	12.6	3005	10.2	2431	10.7	2558	6.5
85			12.6	3016	11.5	2742	7.4
86			9.2	2195	8.9	2121	5.6
87	13.0	3113	12.9	3087	12.0	2867	7.6
88	14.1	3376	13.8	3299	13.5	3234	8.3
89			9.3	2216	9.0	2161	5.7
90			10.4	2482	11.1	2650	6.7
91			10.3	2459	10.9	2608	6.6
92	12.2	2924	12.3	2940	10.9	2605	7.2
93			9.2	2195	8.9	2121	5.6
94	14.1	3380	12.9	3082	10.8	2582	7.5
95	11.4	2719	9.2	2206	9.0	2140	5.6
96	15.6	3727	14.0	3358	12.8	3068	8.6
97	13.6	3240	12.4	2969	9.9	2376	7.0
98	11.8	2809	9.5	2282	9.6	2285	5.9
99			13.3	3186	11.6	2767	7.9
100	12.9	3086	12.8	3068	11.9	2854	7.6
101	11.6	2783	9.5	2265	9.5	2274	5.9
102	12.4	2962	11.5	2752	8.2	1964	6.2
103	14.4	3441	13.1	3129	11.2	2667	7.7
104	11.2	2672	9.1	2170	8.7	2072	5.5
105			9.2	2188	8.8	2108	5.5
106	14.8	3549	13.4	3207	11.7	2805	8.0
107	12.2	2923	10.0	2383	10.3	2470	6.3
108	14.7	3512	13.4	3192	11.6	2777	7.9
109	13.1	3131	10.6	2523	11.4	2722	6.9
110	13.3	3169	10.6	2538	11.5	2750	6.9
111	13.0	3114	12.1	2896	9.4	2240	6.7
112	11.1	2647	11.2	2682	8.4	2004	6.2
113	12.9	3081	12.1	2896	9.4	2240	6.7
114	12.3	2931	11.6	2772	8.4	2004	6.2

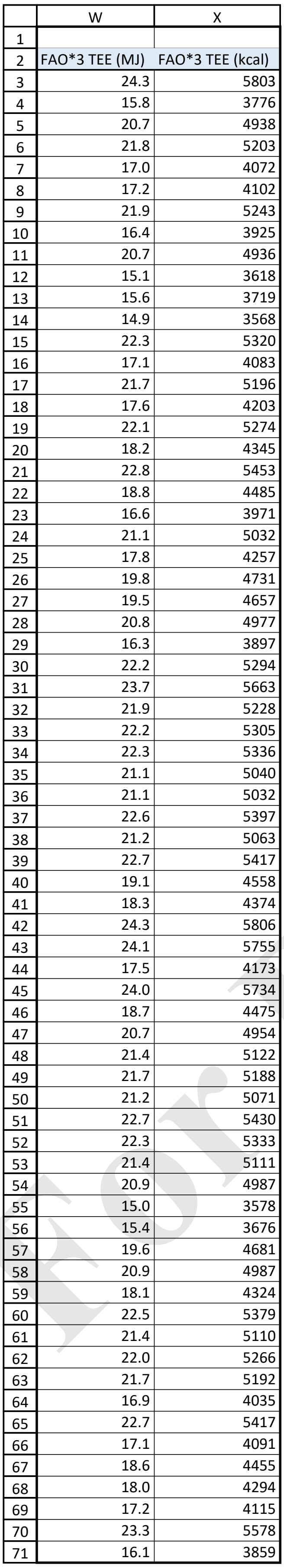
TEE estimations

	P	Q	R	S	T	U	V
1							
2	RMR from FAO (kcal)	FAO*1.89 TEE (MJ)	FAO*1.89 TEE (kcal)	FAO*2 TEE (MJ)	FAO*2 TEE (kcal)	FAO*2.5 TEE (MJ)	FAO*2.5 TEE (kcal)
3	1934	15.3	3656	16.2	3869	20.2	4836
4	1259	10.0	2379	10.5	2517	13.2	3147
5	1646	13.0	3111	13.8	3292	17.2	4115
6	1734	13.7	3278	14.5	3469	18.1	4336
7	1357	10.7	2565	11.4	2714	14.2	3393
8	1367	10.8	2584	11.4	2735	14.3	3418
9	1748	13.8	3303	14.6	3495	18.3	4369
10	1308	10.3	2473	10.9	2617	13.7	3271
11	1645	13.0	3109	13.8	3290	17.2	4113
12	1206	9.5	2279	10.1	2412	12.6	3015
13	1240	9.8	2343	10.4	2479	13.0	3099
14	1189	9.4	2248	10.0	2378	12.4	2973
15	1773	14.0	3352	14.8	3547	18.5	4433
16	1361	10.8	2572	11.4	2722	14.2	3402
17	1732	13.7	3273	14.5	3464	18.1	4330
18	1401	11.1	2648	11.7	2802	14.7	3502
19	1758	13.9	3322	14.7	3516	18.4	4395
20	1448	11.5	2737	12.1	2897	15.1	3621
21	1818	14.4	3436	15.2	3635	19.0	4544
22	1495	11.8	2826	12.5	2990	15.6	3738
23	1324	10.5	2502	11.1	2647	13.8	3309
24	1677	13.3	3170	14.0	3354	17.5	4193
25	1419	11.2	2682	11.9	2838	14.8	3547
26	1577	12.5	2980	13.2	3154	16.5	3942
27	1552	12.3	2934	13.0	3104	16.2	3880
28	1659	13.1	3136	13.9	3318	17.4	4148
29	1299	10.3	2455	10.9	2598	13.6	3248
30	1765	14.0	3335	14.8	3529	18.5	4412
31	1888	14.9	3568	15.8	3775	19.7	4719
32	1743	13.8	3293	14.6	3485	18.2	4356
33	1768	14.0	3342	14.8	3537	18.5	4421
34	1779	14.1	3362	14.9	3557	18.6	4447
35	1680	13.3	3175	14.1	3360	17.6	4200
36	1677	13.3	3170	14.0	3354	17.5	4193
37	1799	14.2	3400	15.1	3598	18.8	4497
38	1688	13.3	3190	14.1	3375	17.7	4219
39	1806	14.3	3413	15.1	3611	18.9	4514
40	1519	12.0	2872	12.7	3039	15.9	3799
41	1458	11.5	2756	12.2	2916	15.3	3645
42	1935	15.3	3658	16.2	3871	20.2	4839
43	1918	15.2	3626	16.1	3837	20.1	4796
44	1391	11.0	2629	11.6	2782	14.5	3477
45	1911	15.1	3613	16.0	3823	20.0	4779
46	1492	11.8	2819	12.5	2983	15.6	3729
47	1651	13.1	3121	13.8	3303	17.3	4129
48	1707	13.5	3227	14.3	3415	17.9	4268
49	1729	13.7	3268	14.5	3459	18.1	4323
50	1690	13.4	3195	14.1	3381	17.7	4226
51	1810	14.3	3421	15.1	3620	18.9	4525
52	1778	14.1	3360	14.9	3556	18.6	4445
53	1704	13.5	3220	14.3	3407	17.8	4259
54	1662	13.1	3142	13.9	3324	17.4	4156
55	1193	9.4	2254	10.0	2385	12.5	2981
56	1225	9.7	2316	10.3	2451	12.8	3064
57	1560	12.3	2949	13.1	3120	16.3	3901
58	1662	13.1	3142	13.9	3325	17.4	4156
59	1441	11.4	2724	12.1	2883	15.1	3603
60	1793	14.2	3389	15.0	3586	18.8	4483
61	1703	13.5	3219	14.3	3407	17.8	4258
62	1755	13.9	3318	14.7	3511	18.4	4388
63	1731	13.7	3271	14.5	3461	18.1	4326
64	1345	10.6	2542	11.3	2690	14.1	3363
65	1806	14.3	3413	15.1	3611	18.9	4514
66	1364	10.8	2577	11.4	2727	14.3	3409
67	1485	11.7	2807	12.4	2970	15.5	3712
68	1431	11.3	2705	12.0	2862	15.0	3578
69	1372	10.8	2593	11.5	2744	14.3	3430
70	1859	14.7	3514	15.6	3719	19.4	4648
71	1286	10.2	2431	10.8	2572	13.5	3215

TEE estimations

	P	Q	R	S	T	U	V
72	1507	11.9	2848	12.6	3014	15.8	3767
73	1633	12.9	3086	13.7	3266	17.1	4082
74	1833	14.5	3464	15.3	3666	19.2	4583
75	1935	15.3	3658	16.2	3871	20.2	4839
76	1833	14.5	3464	15.3	3666	19.2	4583
77	1864	14.7	3522	15.6	3727	19.5	4659
78	1413	11.2	2670	11.8	2825	14.8	3532
79	1468	11.6	2775	12.3	2936	15.4	3670
80	1466	11.6	2771	12.3	2932	15.3	3665
81	1833	14.5	3464	15.3	3666	19.2	4583
82	1901	15.0	3593	15.9	3803	19.9	4753
83	1607	12.7	3037	13.4	3214	16.8	4017
84	1555	12.3	2939	13.0	3110	16.3	3887
85	1776	14.0	3357	14.9	3552	18.6	4440
86	1330	10.5	2514	11.1	2661	13.9	3326
87	1828	14.5	3455	15.3	3656	19.1	4570
88	1985	15.7	3752	16.6	3970	20.8	4963
89	1351	10.7	2552	11.3	2701	14.1	3376
90	1604	12.7	3031	13.4	3208	16.8	4010
91	1582	12.5	2989	13.2	3163	16.5	3954
92	1720	13.6	3250	14.4	3439	18.0	4299
93	1330	10.5	2514	11.1	2661	13.9	3326
94	1791	14.2	3384	15.0	3581	18.7	4477
95	1340	10.6	2533	11.2	2680	14.0	3350
96	2058	16.3	3889	17.2	4116	21.5	5145
97	1681	13.3	3178	14.1	3363	17.6	4204
98	1413	11.2	2671	11.8	2827	14.8	3534
99	1891	15.0	3574	15.8	3782	19.8	4728
100	1823	14.4	3445	15.3	3646	19.1	4557
101	1408	11.1	2661	11.8	2816	14.7	3520
102	1470	11.6	2779	12.3	2941	15.4	3676
103	1837	14.5	3471	15.4	3673	19.2	4591
104	1306	10.3	2468	10.9	2612	13.7	3265
105	1324	10.5	2502	11.1	2648	13.8	3310
106	1912	15.1	3613	16.0	3824	20.0	4780
107	1509	11.9	2852	12.6	3018	15.8	3773
108	1897	15.0	3585	15.9	3794	19.8	4742
109	1642	13.0	3104	13.7	3285	17.2	4106
110	1657	13.1	3132	13.9	3314	17.3	4143
111	1611	12.7	3044	13.5	3221	16.8	4027
112	1481	11.7	2799	12.4	2962	15.5	3703
113	1611	12.7	3044	13.5	3221	16.8	4027
114	1490	11.8	2817	12.5	2980	15.6	3726

TEE estimations

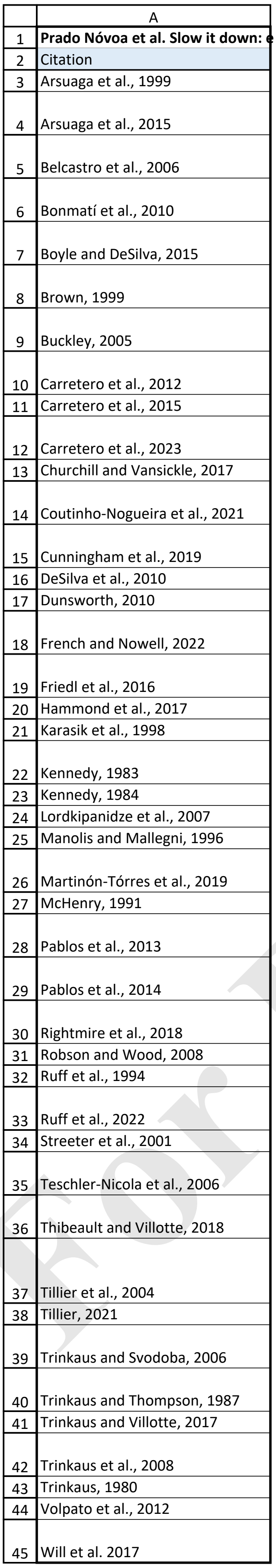


	W	X
1		
2	FAO*3 TEE (MJ)	FAO*3 TEE (kcal)
3	24.3	5803
4	15.8	3776
5	20.7	4938
6	21.8	5203
7	17.0	4072
8	17.2	4102
9	21.9	5243
10	16.4	3925
11	20.7	4936
12	15.1	3618
13	15.6	3719
14	14.9	3568
15	22.3	5320
16	17.1	4083
17	21.7	5196
18	17.6	4203
19	22.1	5274
20	18.2	4345
21	22.8	5453
22	18.8	4485
23	16.6	3971
24	21.1	5032
25	17.8	4257
26	19.8	4731
27	19.5	4657
28	20.8	4977
29	16.3	3897
30	22.2	5294
31	23.7	5663
32	21.9	5228
33	22.2	5305
34	22.3	5336
35	21.1	5040
36	21.1	5032
37	22.6	5397
38	21.2	5063
39	22.7	5417
40	19.1	4558
41	18.3	4374
42	24.3	5806
43	24.1	5755
44	17.5	4173
45	24.0	5734
46	18.7	4475
47	20.7	4954
48	21.4	5122
49	21.7	5188
50	21.2	5071
51	22.7	5430
52	22.3	5333
53	21.4	5111
54	20.9	4987
55	15.0	3578
56	15.4	3676
57	19.6	4681
58	20.9	4987
59	18.1	4324
60	22.5	5379
61	21.4	5110
62	22.0	5266
63	21.7	5192
64	16.9	4035
65	22.7	5417
66	17.1	4091
67	18.6	4455
68	18.0	4294
69	17.2	4115
70	23.3	5578
71	16.1	3859

TEE estimations

	W	X
72	18.9	4520
73	20.5	4898
74	23.0	5499
75	24.3	5806
76	23.0	5499
77	23.4	5591
78	17.7	4238
79	18.4	4404
80	18.4	4398
81	23.0	5499
82	23.9	5704
83	20.2	4821
84	19.5	4665
85	22.3	5328
86	16.7	3991
87	22.9	5484
88	24.9	5955
89	17.0	4052
90	20.1	4812
91	19.9	4745
92	21.6	5159
93	16.7	3991
94	22.5	5372
95	16.8	4020
96	25.8	6174
97	21.1	5044
98	17.7	4240
99	23.7	5673
100	22.9	5469
101	17.7	4223
102	18.5	4411
103	23.1	5510
104	16.4	3918
105	16.6	3971
106	24.0	5735
107	18.9	4527
108	23.8	5690
109	20.6	4927
110	20.8	4972
111	20.2	4832
112	18.6	4443
113	20.2	4832
114	18.7	4471

References



	A
1	**Prado Nóvoa et al. Slow it down:**
2	Citation
3	Arsuaga et al., 1999
4	Arsuaga et al., 2015
5	Belcastro et al., 2006
6	Bonmatí et al., 2010
7	Boyle and DeSilva, 2015
8	Brown, 1999
9	Buckley, 2005
10	Carretero et al., 2012
11	Carretero et al., 2015
12	Carretero et al., 2023
13	Churchill and Vansickle, 2017
14	Coutinho-Nogueira et al., 2021
15	Cunningham et al., 2019
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19	Friedl et al., 2016
20	Hammond et al., 2017
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30	Rightmire et al., 2018
31	Robson and Wood, 2008
32	Ruff et al., 1994
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34	Streeter et al., 2001
35	Teschler-Nicola et al., 2006
36	Thibeault and Villotte, 2018
37	Tillier et al., 2004
38	Tillier, 2021
39	Trinkaus and Svodoba, 2006
40	Trinkaus and Thompson, 1987
41	Trinkaus and Villotte, 2017
42	Trinkaus et al., 2008
43	Trinkaus, 1980
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Supplementary Online Material (SOM):

Slow it down: evolution of human metabolism over two million years.

SOM Table S1.

Hominins database (uploaded as an Excel)

SOM Table S2.

Characteristics of the different equations applied to estimate total energy expenditure (TEE), in MJ/day except when indicated in other units. Sex= females (♀), males (♂). BM= body mass in kilograms; RMR= Resting Metabolic Rate; PAL= Physical activity level; Height in centimeters; Age in years. FAO= FAO/WHO/UNU, 2004; Leonard= Leonard & Robertson, 1997; Pontzer= Pontzer et al., 2021; Vinken= Vinken et al., 1999.

Model	Sex	Age (years)	RMR	TEE		
FAO (RMR) (kcal)	♀	18-29	= 14.818 * BM + 486.6	RMR * PAL	PAL =	1.89
		30-60	= 8.126 * BM + 845.6			2.0
	♂	18-29	= 15.057 * BM + 692.2			2.5
		30-60	= 11.472 * BM + 873.1			3.0
Leonard (kcal)	♀&♂	-	-	= 86.0 * BM ^ 0.793		
Pontzer (MJ)	♀&♂	20-60	-	= 5.984 + 0.065 * BM + 2.669 * Sex (females= 0; males= 1) – 0.025 * Age		
Vinken (MJ)	♀&♂	18-81	-	= 7.377 - 0.073 * Age + 0.0806 * BM + 0.0135 * Height – 1.363 * Sex (females= 1; males= 0)		

SOM References

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