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REVIEW

Title: Review: The different adaptive trajectories in Neanderthals and *Homo sapiens* and their implications for contemporary human physiological variation

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15 **Abstract:** Neanderthals are our one of our closest evolutionary cousins, but while they evolved in
16 Eurasia, we (anatomically modern humans, AMH) originated in Africa. This contrasting evolutionary
17 history has led to morphological and genetic distinctions between our species. Neanderthals are
18 characterised by a relatively stocky build, high body mass, proportionally wide bodies and shorter
19 limbs, a bell-shaped ribcage with a wide pelvis, and a long, low cranial vault compared with AMH.
20 Classic readings of Neanderthal morphology link many of these traits to cold climate adaptations,
21 however these interpretations have been questioned and alternative hypotheses including
22 behavioural factors, dietary adaptations, locomotor specialisations, evolutionary history and neutral
23 evolutionary processes have been invoked. Compared with AMH, Neanderthals may have been
24 adapted for strength and power rather than endurance and may have consumed a diet high in
25 animal products. However, reviewing these hypotheses highlights a number of limitations in our
26 understanding of contemporary human physiology and metabolism, including the relationship
27 between climate and morphology in AMH and Neanderthals, physiological limits on protein
28 consumption, and the relationship between gut morphology and diet. As various relevant factors are
29 clearly linked (e.g. diet, behaviour, metabolism, morphology, activity), ultimately a more integrated
30 approach may be needed to fully understand Neanderthal biology. Variation among contemporary
31 AMHs may offer, with caveats, a useful model for understanding the evolution of both Neanderthal
32 and modern human characteristics, which in turn may further deepen our understanding of
33 variability within and between contemporary humans.

34

35 Neanderthals; Anatomically modern humans; morphology; climate adaptation; power adaptations;
36 metabolism; diet; physiology; endurance running;

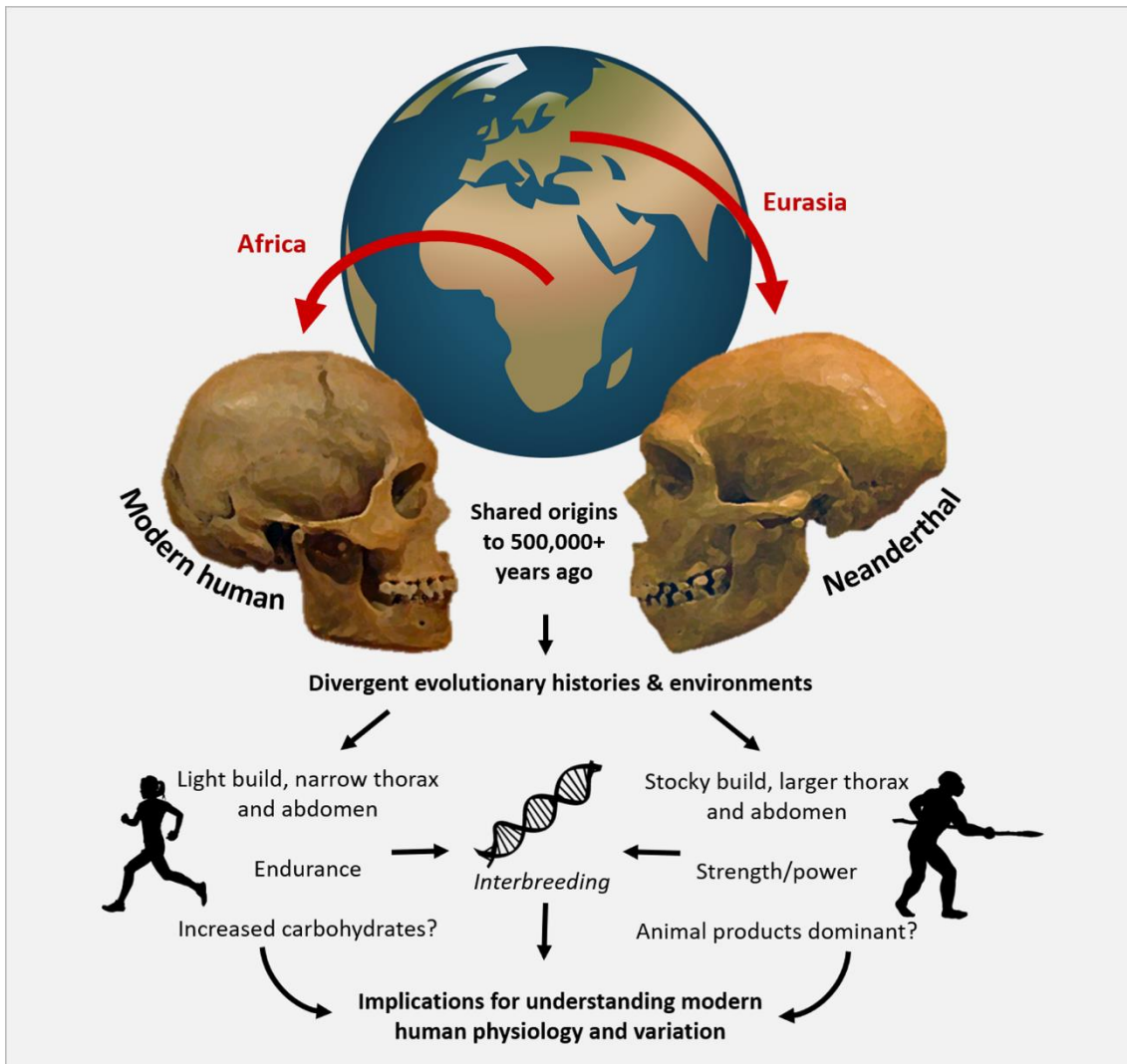
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41 **Graphical abstract:**



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44 **Keywords:** Neanderthals; morphology; climate adaptation; power adaptations; metabolism; diet

45

46 **Abbreviations:** AMH – Anatomically modern human; kya – thousand years ago

47 **Highlights:**

48

- 49 • Neanderthals are one of our closest evolutionary relatives

50

- 51 • Contrasting and parallel evolutionary trajectories of Neanderthals and modern humans offer
52 potential for insight into the evolution of physiology, anatomy and behaviour in both species

53

- 54 • Neanderthal morphology has classically been interpreted as adaptation to cold climate,
55 although high activity levels and muscle mass combined with a power/strength phenotype
56 and diet may be implicated

57

- 58 • Challenges in interpreting Neanderthal adaptations highlight limitations to our
59 understanding of current human diet, metabolism and physiology

60

- 61 • Understanding Neanderthal adaptations and evolution may ultimately help us gain greater
62 insight into human variation and variability in diet, metabolism, physiology, morphology and
63 activity

64 **Introduction**

65

66 The shared and yet distinct evolutionary trajectories of anatomically modern humans (*Homo*
67 *sapiens*, hereafter AMH) and our closest evolutionary relatives, the Neanderthals, provide a valuable
68 comparative context for understanding diversity and adaptation in anatomy, physiology and
69 behaviour in the recent history of our evolutionary lineage. The contrasting biology and evolutionary
70 contexts of these two groups may also shed light on the evolution and/or functional significance of
71 anatomical and physiological traits in humans alive today. This is all the more relevant in light of
72 evidence for interbreeding between Neanderthals and AMH, such that typical individuals with
73 ancestry outside of Africa carry 1-3% in a geographically patterned manner, and modern-day
74 Africans also show a trace, albeit more limited, of Neanderthal heritage (Fu et al., 2015; Green et al.,
75 2010; Kuhlwilm et al., 2016; Posth et al., 2017; Prüfer et al., 2017; Racimo et al., 2015; Sankararaman
76 et al., 2014; Villanea and Schraiber, 2019). Various studies have argued that Neanderthal ancestry in
77 contemporary individuals has a range of implications for health, physiology, and morphology (Harris
78 and Nielsen, 2016; Racimo et al., 2015; Reilly et al., 2022; Zeberg and Pääbo, 2020, 2021), and it is
79 plausible that Neanderthal-derived genes impact physiology and athletic performance. This review
80 will give an overview of the nature and evolution of differences in the anatomy and physiology
81 between AMH and Neanderthals, and consider the implications of Neanderthal ancestry on variation
82 in the physiology, metabolism and anatomy of contemporary populations. While physiology is
83 difficult to infer from fossil remains alone, anatomical variation and other analyses of
84 palaeoanthropological and archaeological evidence can give insights into aspects of physiology in
85 recent hominins such as Neanderthals, and may be augmented by our growing understanding of
86 genetic variability in this extinct group.

87

88 **Origins of Neanderthals and modern humans**

89

90 Neanderthals (*Homo neanderthalensis*) were the first fossil species to be identified as extinct
91 hominins¹ (King, 1864), and are one of our closest evolutionary cousins. Our own species AMH,
92 Neanderthals, and a more recently-discovered lineage from Asia known as Denisovans, likely shared
93 a common ancestor between approximately 550 and 750 thousand years ago (kya) (Prüfer et al.,
94 2014), or possibly earlier (Gómez-Robles, 2019). Neanderthals evolved in Western Eurasia, and
95 occupied a wide geographic range from modern day Wales to southwest Asia and the Urals (Figure
96 1). While the underlying evolutionary pattern is debated (Dean et al., 1998; Hublin, 2009; Rosas et
97 al., 2019), Neanderthal characteristics appear from around 430 kya among the Sima de los Huesos
98 hominins from modern-day Spain (Arsuaga et al. 2014; 2015), while it is widely considered that a
99 consistent morphological pattern defining Neanderthals appeared from around 300-250 kya, and so
100 called 'classic' Neanderthal morphology evolved by around 70 kya (reviewed in Rosas et al., 2022).
101



102
103 Figure 1: Map of Eurasia showing the extent of the known Neanderthal range (modified from
104 https://commons.wikimedia.org/wiki/File:Range_of_Neanderthals.png, under CC BY-SA 3.0).
105

¹ Hominins are members of the evolutionary lineage leading to anatomically modern humans since its split from the lineage leading to our closest living relatives, chimpanzees and bonobos

106 In parallel, AMH evolved at the same time in Africa. The earliest evidence for AMH is debated, but
107 fossils from Jebel Iroud, Morocco dating to 315 kya (Hublin et al., 2017; Richter et al., 2017), Omo
108 Kibish, Ethiopia at ~230 kya (Vidal et al., 2022), and Florisbad in South Africa at ~259 kya all show
109 AMH traits, although the trend towards gracilisation of the skeleton and globularisation of the
110 cranial vault (see below) is evident much later in the evolution of our species (Neubauer et al., 2018;
111 Ruff, 2005). The first substantial European occupations by AMH migrating from Africa date to around
112 43 kya (Fewlass et al., 2020; Higham et al., 2011; Hublin et al., 2020; although earlier intermittent
113 occupations are known e.g. at Mandrin, France: Slimak et al., 2022). Neanderthals became extinct
114 around 40 kya (Higham et al., 2014), leading some to argue for a link between these events (Gilpin et
115 al., 2016; Melchionna et al., 2018; Sørensen, 2011; Timmermann, 2020). This contrast in early
116 evolutionary environments of Neanderthals (cold/temperate environments) and AMH
117 (topical/subtropical Africa) likely drove key differences in the morphology, physiology and behaviour
118 of these groups, with geographic isolation and neutral evolutionary processes also likely playing
119 some role (Churchill, 2014; Rosas et al., 2022; Weaver, 2009).

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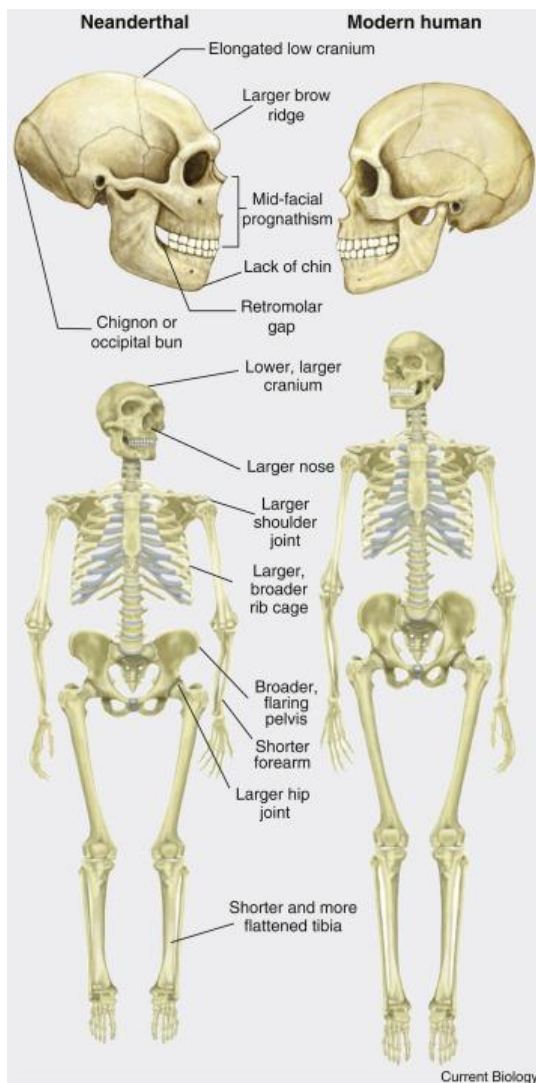
122 **Neanderthals and modern human anatomy: contrasting evolutionary trajectories**

123

124 While Denisovans and Neanderthals share a more recent common ancestor with each other than
125 either does with AMH (Reich et al., 2010), the Denisovans were discovered relatively recently and
126 their morphology is poorly characterised, in contrast with Neanderthals. Thus, while comparisons
127 with Denisovans could be equally informative, a lack of documented anatomical traits for
128 Denisovans prohibits such comparisons at present. Perhaps the most striking contrast between
129 Neanderthal and AMH anatomy is the relative gracility of the AMH skeleton. While the robustness
130 and 'heavy-build' of the Neanderthal frame is often commented on, in the context of hominin
131 evolution, skeletal robustness seems to be the ancestral state, and it is AMH who are unusual in the

132 lightness of our build (Ruff, 2005; Ruff et al., 1993). Indeed, the stockier build, broader pelvis and
133 broad, deep thorax of Neanderthals seem to be an ancestral trait that can be traced back to our
134 Early and Middle Pleistocene hominin ancestors, while it is AMH that are likely derived in terms of
135 our narrower pelvis and reduced ribcage volume (Arsuaga et al.,1999, 2010, 2015; Bonmatí et al.,
136 2010; Bastir et al., 2020). While this review will focus on traits linked to physiology, physical
137 performance and metabolism, a brief overview of the classic Neanderthal and AMH traits is
138 warranted here (Figure 2).

139



140 Figure 2: Key differences between Neanderthals and anatomically modern humans in their skeletal
141 biology (reproduced with permission from Reilly et al., 2022, Figure 1,)

142

143 In the craniofacial skeleton, Neanderthals share a similar brain volume to AMH, but a notable
144 difference in cranial vault (and by inference brain) shape with a receding frontal bone and distinctive
145 occipital bun, possibly implying some differences in cognitive capacity, although it is notable that
146 early AMH share this brain shape up until about 100kya (Neubauer et al., 2018). The Neanderthal
147 skull is also characterised by a marked brow ridge, midfacial prognathism (projection in the midface
148 and nasal area), and a lack of chin (reviewed in Churchill, 2014; Rosas et al., 2022).

149

150 In the postcranial skeleton, Neanderthals are again characterised by general robustness. Their
151 bodies were broader than those of AMH, reflected in the dimensions of the pelvis and ribcage
152 (reviewed in Churchill, 2014; Rosas et al., 2022), while their limbs were proportionally shorter
153 especially in their distal long bones of the lower limb (Holliday 1997a; Trinkaus, 1981). The
154 difference is particularly marked in comparison to the earliest Upper Palaeolithic AMH in Eurasia,
155 who maintain intralimb proportions more similar to extant African populations (Holliday, 1997a).
156 More detailed features of the shoulder, spine, hand and foot anatomy are thought to reflect
157 adaptations for specific hunting tasks, manipulation and locomotor abilities (Churchill, 2014; Rosas
158 et al., 2022; Weaver, 2009), while some characteristics represent byproducts of changes in other
159 anatomical regions, as has been argued for the cervical spine in relation to cranial morphology
160 (Gómez-Olivencia et al., 2013), or likely reflect the impacts of random genetic drift (Churchill, 2014;
161 Rosas et al., 2022; Weaver, 2009). This is particularly pertinent given genetic and skeletal evidence
162 indicates relatively small population size and signals of inbreeding among Neanderthals that may
163 have played a role in their ultimate extinction (Kuhlwilm et al., 2016; Lalueza-Fox et al., 2011; Prüfer
164 et al., 2017; Ríos et al., 2019).

165

166 Estimates based on skeletal dimensions indicate that Neanderthals were slightly shorter but
167 significantly heavier on average than Palaeolithic AMH, with mean statures in the region of 1.62-1.66
168 m and 1.52-1.57 m for Neanderthal males and females (Churchill, 2014; Rosas et al., 2022), and

169 mean body mass around 78-82 kg and 66 kg for Neanderthal males and females respectively
170 (Churchill, 2014; Plavcan et al., 2014; Rosas et al., 2022; Ruff, 1991). The estimation of body
171 composition based on skeletal data is unreliable at best (see Pomeroy et al., 2018), but assuming
172 that Neanderthals were relatively lean due to their active lifestyles and unprocessed diets, this
173 greater relative body mass compared with AMH indicates substantially higher body mass and
174 particularly lean tissue mass, with implications for a substantially greater total energy expenditure
175 and nutritional requirements in Neanderthals than in AMH (Churchill, 2014; Froehle and Churchill,
176 2009; Ocobock et al., 2021).

177

178

179 **Climate and the classic explanation of Neanderthal physique**

180

181 Interpretations of the differences between Neanderthal and AMH anatomy have been interpreted as
182 reflecting their differing evolutionary origins and histories. The stocky build, short limbs and high
183 body mass of Neanderthals, as well as their large and prominent noses and frontal sinuses have
184 been traditionally linked to their evolution in the glacial environments of Western Eurasia (Churchill,
185 1998; Churchill, 2014; Holliday, 1997b; Steegmann et al., 2002; Trinkaus, 1981; Wroe et al., 2018),
186 while the origins of AMH in the hotter tropical climates of Africa (Hanna and Brown, 1983) are
187 thought to explain their lighter body mass and smaller nose. These characteristic patterns of limb
188 proportions and body mass are often considered to be consistent with the ecogeographic 'rules' of
189 Bergmann (1847) and Allen (1877). Bergmann's 'rule' predicts greater body mass among mammals
190 inhabiting colder environments compared with closely related species in warmer environments in
191 order to minimise heat loss by reducing the surface area: volume ratio, while Allen's 'rule' predicts
192 proportionally shorter extremities in cold environments for the same reason. To some extent, the
193 elevated body mass, shorter limb proportions and nasal morphology among Neanderthals echo
194 those of recent human populations living at in cold environments at high latitudes (Churchill, 1998;

195 Churchill, 2014; Ocobock et al., 2021; Trinkaus, 1981), albeit more extreme and leading
196 Neanderthals to be characterised as ‘hyper-polar’ in their body proportions (Trinkaus, 1981; Weaver,
197 2003, 2009). For example, compared with recent human populations inhabiting the Arctic,
198 Neanderthals averaged a similar stature but had 10-25% greater body mass (data in Churchill, 2014
199 Table 4.2).

200

201

202 **Beyond climate: behavioural interpretations of Neanderthal physique**

203

204 While the climatic interpretation of key Neanderthal and AMH traits may be partially correct
205 (Churchill, 2014; Collard and Cross, 2017; Ocobock et al., 2021; Weaver, 2003, 2009; Wroe et al.,
206 2018), the extent to which recent AMH populations actually follow the classic ecogeographic rules of
207 Bergmann (1847) and Allen (1877) has been increasingly challenged. Variation in body mass and
208 proportions among recent AMH and Neanderthals appear to follow these patterns (Foster and
209 Collard, 2013; Katzmarzyk and Leonard, 1998; Roberts, 1953; Roberts, 1978; Ruff, 1991; Trinkaus,
210 1981), although Walker et al. (2011) point out that the apparently ‘Arctic’ limb proportions of
211 Palomas 96 female from southern Iberia may question this interpretation for Neanderthals at least.
212 Furthermore, incorporating the effects of population history or shared ancestry substantially weaken
213 or even remove relationships between body size and proportions or climate in recent AMH
214 populations (Pomeroy et al., 2021; Roseman and Auerbach, 2015; Savell et al., 2016; Savell et al.,
215 2022), implying important roles of neutral evolutionary processes in accounting for these so-called
216 ecogeographic rules and potentially calling into question the classic climatic interpretation of the
217 proportionally short limbs and high body mass of Neanderthals.

218

219 Similarly, correlations between phenotype and climate may reflect the influence of variables that
220 covary with climate (e.g. pathogen load, environmental productivity), rather than the direct effects

221 of climate per se (Pomeroy et al., 2021; Wells et al., 2019; Wells and Cortina-Borja, 2013). It has
222 been well documented that body mass, relative limb and trunk proportions, and proportions of
223 different limb segments (e.g. the femur vs the tibia) are highly plastic and sensitive to the effects of
224 poor nutrition, disease and other adverse environmental conditions during development (Bailey et
225 al., 2007; Pomeroy et al., 2012; Wadsworth et al., 2002). Furthermore, empirical work examining the
226 impacts of body shape differences on heat dissipation, while limited, have failed to support the
227 benefits of shorter lower leg relative to the thigh for heat retention in cold environments (Tilkens et
228 al., 2007). Some have abandoned the relevance of Bergmann's rule to humans altogether (Bogin et
229 al., 2022) because of the profound effects of socioeconomic status, nutrition and other variables on
230 body size. Evidence does seem to support a relationship between body breadth and climate in
231 recent AMH populations (Ruff, 1991; Savell et al., 2022), even if a relationship between climate and
232 limb proportions is not (Savell et al., 2022). However, a different situation may describe variation
233 among Neanderthals, as there is evidence for a temporal trend towards narrower pelvises in the
234 Neanderthal lineage that is not easily explained by climatic variation (Bonmatí et al., 2010; Arsuaga
235 et al., 2015).

236

237 This debate over the impact of climate on recent human phenotype casts doubt on whether climatic
238 variables can account for the differences in physique between AMH and Neanderthals. Furthermore,
239 whether these intra-specific patterns in recent AMH are applicable to interspecific comparisons
240 between AMH and Neanderthals requires greater critical evaluation. Alternative hypotheses linking
241 Neanderthal physique with behaviour and activity have been proposed, and merit further review
242 and testing in light of these doubts. The proportionally shorter distal lower limb segments of
243 Neanderthals, for example, have been theoretically linked to greater locomotor efficiency over
244 steeper terrain (Higgins and Ruff, 2011). Neanderthals have been interpreted as being more highly
245 mobile than many Upper Pleistocene AMH based on the cross-sectional geometry of lower limb
246 bones (Shaw and Stock, 2013), and the theoretical demands of acquiring sufficient food in the

247 resource-sparse environments of glacial Eurasia (Froehle and Churchill, 2009; Ocobock et al., 2021).
248 However, the advantage of shortened distal lower limbs in steep terrain has not been empirically
249 demonstrated, and the apparent association between Neanderthal remains and more rugged
250 environments may reflect the greater chance of preservation in caves, which are associated with
251 steep topography (Ocobock et al., 2021).

252

253 Other aspects of Neanderthal morphology have been linked to their greater body mass and perhaps
254 greater activity levels. In particular, the broader and more bell-shaped ribcage (Franciscus and
255 Churchill, 2002; García-Martínez et al., 2014, 2018; Gómez-Olivencia et al., 2009, 2018; Sawyer and
256 Maley, 2005), larger projecting nose and larger internal nasal cavity dimensions may reflect a need
257 for increased oxygen supply to fuel the greater metabolic demands of higher body mass among
258 Neanderthals. While larger airways and lung volume (reflected in nasal and ribcage shape) could
259 theoretically reflect a need for greater respiratory capacity, again the metabolic advantages of these
260 characteristics are yet to be tested empirically in recent AMH (Ocobock et al., 2021) and some
261 studies suggest that proportional to body mass, Neanderthals do not have greater lung volumes
262 than AMH (Arensburg, 1991; Franciscus and Churchill, 2002; García-Martínez et al., 2014). It is also
263 notable that a larger thorax seems to be an ancestral trait inherited from Early and Middle
264 Pleistocene hominins (Asuaga et al. 2015; Gómez-Olivencia et al., 2018; Bastir et al. 2020), and so
265 evolutionary history may also explain the larger thorax of Neanderthals.

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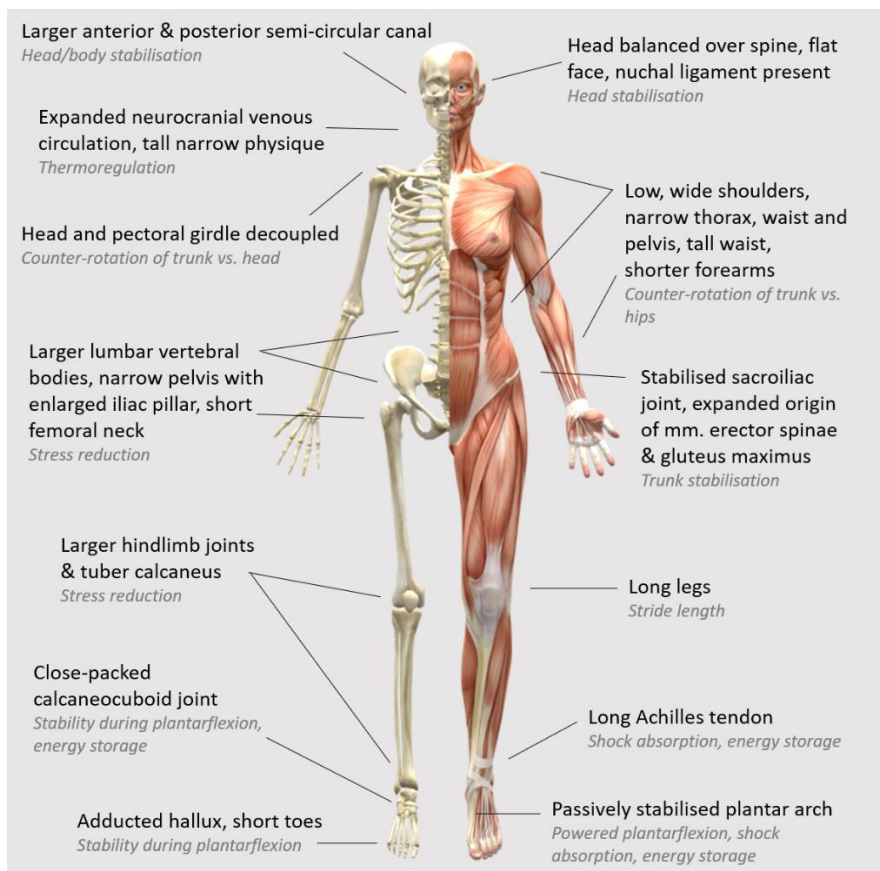
268 **Contrasting locomotor adaptations: Neanderthal sprinters and AMH distance runners**

269

270 An alternative interpretation of Neanderthal-AMH contrasts in body build and proportionality may
271 be adaptation to different locomotor specialisms: Neanderthals to short sprints and hunting large
272 prey at close proximity (Ochando et al., 2019; Stewart et al., 2019), versus AMH specialising in

273 distance running and the pursuit of prey to exhaustion (Bramble and Lieberman, 2004; Lieberman et
 274 al., 2009). Bramble and Lieberman (2004; Lieberman et al., 2009) have argued that AMH possess a
 275 suite of traits that make us adapted for endurance running (Figure 3), including adaptations to
 276 stabilize the head (e.g., characteristics of the nuchal ligament, inner ear, orthognathic (flat) face), a
 277 narrow waist, tall stature, large lower limb joints with proportionally long limbs, long Achilles
 278 tendons, and spring-like plantar arches (Bramble and Lieberman, 2004).

279



280

281 Figure 3: Characteristics of anatomically modern humans, some shared with other members of the
 282 genus *Homo*, that are proposed adaptations to endurance running, based on Bramble and
 283 Lieberman (2004, Table 1). Traits are labelled in black, and their inferred function in grey text. Image
 284 based on Ryan Hoyme (massagenerds) - [https://pixabay.com/en/muscles-skeleton-half-body-](https://pixabay.com/en/muscles-skeleton-half-body-2277447/)
 285 [2277447/](https://pixabay.com/en/muscles-skeleton-half-body-2277447/) archive copy, CC0, <https://commons.wikimedia.org/w/index.php?curid=74822435>.

286

287 When this adaptation to long distance running evolved remains unclear, but it should already be
288 apparent from the discussion above that Neanderthals do not show these characteristics to as great
289 an extent as AMH and so may not be so clearly adapted for endurance running. Other Neanderthal
290 characteristics support this interpretation: for example, they have a longer calcaneus, which
291 increases the moment arm of the Achilles tendon and so decreases the efficiency of long distance
292 running (Raichlen et al., 2011). Similarly, the specialisation of AMH for endurance running would
293 explain the spread within our species of a null mutation in the *ACTN3* gene associated with a high
294 percentage of slow-twitch muscle fibres thought to be advantageous for endurance running (Yang et
295 al., 2003). Genetic evidence suggests that this null mutation spread among modern humans around
296 50 kya with the Out of Africa dispersals of AMH (Friedlander et al., 2013). The frequency of the
297 *ACTN3* null allele varies geographically in contemporary humans, with higher frequencies in
298 European and Asian populations, which may suggest that it offers advantages for thermoregulation
299 in colder and/or energy economy in resource-poor environments (Friedlander et al., 2013; Head et
300 al., 2015). Alternatively, genetic drift may explain the allele's modern distribution (Mörseburg et al.,
301 2022). Furthermore, recent work with human endurance athletes indicates that lower running
302 efficiency in heavier individuals can be compensated for by increasing oxygen usage, though this
303 comes at an energetic cost (Longman et al., 2022), a particularly interesting observation given
304 observations about Neanderthal respiratory capacities.

305

306 Exploring more genetic variants associated with power and strength phenotypes (i.e., phenotypes
307 associated with muscular power rather than endurance) in recent AMH, Stewart and colleagues
308 (2019) have argued that Neanderthals (n=9) show higher frequencies of 39 alleles associated with
309 power phenotypes in modern human athletes (Ahmetov et al., 2016) than in a sample of recent
310 AMH (n=2507). While the usual caveats regarding sample size and whether genetic variants in recent
311 AMH had the same function in Neanderthals, this would support the scenario that a range of
312 Neanderthal characteristics reflect adaptation to power phenotypes (Stewart et al., 2019). However,

313 in relation to the *ACTN3*, it is notable that 3 of the 9 Neanderthals included by Stewart et al. (2019)
314 are heterozygous and one is homozygous for the null allele (for one individual, the genotype could
315 not be determined), so variation at this locus also exists among Neanderthals. Studies of the impacts
316 of the heterozygous condition are inconclusive, but suggest that heterozygotes have an intermediate
317 phenotype (Pasqua et al., 2016). It is also possible that Neanderthals possessed other unique alleles
318 for other loci as yet unidentified that influenced physical performance (Stewart et al., 2019).

319

320 The relationship between Neanderthal skeletal morphology and proposed adaptations for power
321 and strength remains to be fully explored. While testing these proposals is complex since our only
322 experimental subjects are AMH, given the range of variability in human phenotype and especially
323 extreme phenotypes seen among athletes, experimental work with contemporary humans may still
324 be informative (Longman et al., 2020). For example, Bastir and colleagues (2022) reported that, at
325 least in a small sample of contemporary young men, a straighter thoracic spine and narrower, flatter
326 torso are linked to higher running speeds at maximum running velocity and high workloads (though
327 not at lower workloads). They argue this is consistent with a model of power locomotor adaptation
328 in Neanderthals, who are characterised by higher trunk muscularity (inferred from larger skeletal
329 dimensions in the torso) and a straighter thoracic spine. However, the results did not provide
330 support for the flatter, narrower ribcage of AMH being related to endurance running, and some
331 characteristics of Neanderthals, such as reduced lumbar lordosis, are inconsistent with power
332 locomotor adaptations, at least from what we know in modern humans (Bastir et al., 2022).

333

334

335 **Upper body activities and morphology**

336

337 Various characteristics of the Neanderthal upper limb and shoulder girdle have also been
338 interpreted as reflecting a distinct set of behaviours from those of AMH. Most notably, Neanderthals

339 have been characterised as using thrusting spears, rather than thrown projectiles, during hunting
340 (Churchill and Rhodes, 2009; Rhodes and Churchill, 2009). The limited bilateral asymmetry in
341 humeral retroversion in addition to other characters of the upper limb and shoulder (Churchill and
342 Rhodes, 2009; Rhodes and Churchill, 2009), along with archaeological evidence from stone tools
343 (Shea, 2006) and damage to prey bones (Gaudzinski-Windheuser et al., 2018) has supported this
344 interpretation. However, the extent to which Neanderthals threw projectiles remains controversial:
345 experimental evidence (Milks et al., 2019) suggests that Neanderthal spears would have functioned
346 well as projectiles, consistent with some skeletal evidence for habitual throwing at least in some
347 Neanderthals (Favre et al., 2014), and the form and traces of use wear on archaeological tools
348 (Hardy et al., 2013).

349

350 If we accept the evidence that the use of thrusting spears and close-encounter hunting were a
351 regular and significant part of Neanderthal hunting strategies, there are further elements of how the
352 upper limb and shoulder girdle integrate with lower thoracic and pelvic morphology that remain to
353 be explored, and which may help to explain aspects of Neanderthal morphology. Given that a low
354 centre of gravity and an extremely powerful core would presumably be advantageous for certain
355 sports, such as among rugby forwards who play an important role in scrums (actively pushing against
356 opposing forces) and whose success depends on power and strength, such athletes may provide
357 suitable models to begin exploring these relationships between morphology, physique and
358 behaviour. In contemporary AMH, muscle mass is closely related to strength (Frontera et al., 1991)
359 and elite level rugby forwards are typically shorter and stockier than players in other positions
360 (Quarrie et al., 1996), consistent with the model of Neanderthals as adapted for strength and power
361 rather than endurance.

362

363

364 **Diet and metabolism**

365

366 Rather than reflecting an adaptation for greater lung capacity, the Neanderthal ribcage, which is
367 particularly enlarged inferiorly yielding a bell shape (Franciscus and Churchill, 2002; García-Martínez
368 et al., 2014, 2018; Gómez-Olivencia et al., 2009, 2018; Sawyer and Maley, 2005) coupled with their
369 broader pelvis, may alternatively relate to dietary adaptations. Ben-Dor and colleagues (2016) have
370 argued that the Neanderthal ribcage shape and broad pelvis reflect the larger liver and kidneys
371 needed to process their high protein, animal-based diet rather than oxygen demands linked to
372 physique and behaviour. Analyses of stable isotopes from their bones and teeth suggest
373 Neanderthals were top-level carnivores (Jaouen et al., 2022; Richards et al., 2000; Richards and
374 Trinkaus, 2009; Wißing et al., 2019). The fact that in recent humans the development of the lower
375 ribcage is associated with maturation of the digestive tract, while that of the upper ribcage is
376 associated with the maturation of the respiratory system (Bastir et al., 2013) may support this
377 interpretation of Neanderthal lower ribcage morphology.

378

379 Much discussion has also surrounded the likely nature of the Neanderthal diet, which is intimately
380 linked to their physique, physiology and behaviour. The traditional model is that Neanderthals were
381 top level, narrow spectrum hunters eating predominantly meat (Fiorenza et al., 2015; Kuhn and
382 Stiner, 2006), cooperatively hunting medium-large prime age mammals by closely approaching their
383 prey (Berger and Trinkaus, 1995). While stable isotopic analyses of bone and teeth support a highly
384 animal-based diet (Fiorenza et al., 2015; Hardy et al., 2015, 2022; Hockett, 2012), the accuracy of
385 this picture has been questioned on both theoretical and empirical grounds.

386

387 Challenging the interpretation of Neanderthals as inflexible hunters of only medium-large prey,
388 evidence from animal bones recovered from Neanderthal archaeological sites shows that coastal
389 Neanderthal populations hunted and consumed a wider range of animals than previously envisioned
390 including fish, shellfish, crustaceans, and sea mammals (Nabais et al. 2023; Stringer et al., 2008;

391 Zilhão et al., 2020), and others clearly hunted 'low-ranking' small game (Hardy et al., 2013; Stiner,
392 1994) and birds (Blasco and Fernández Peris, 2012; Blasco and Peris, 2009; Gómez-Olivencia et al.,
393 2018.). Nitrogen isotope analyses reflect the protein sources of the diet and may thus not
394 adequately reflect the entire diet if most protein is obtained from animal resources, although more
395 recent compound-specific analysis of nitrogen isotopes which are able to give more specific
396 information on trophic level still indicate that Neanderthals were high in the food chain (Jaouen et al.,
397 2019; Naito et al., 2016).

398

399 From a theoretical perspective, researchers have cast doubt on whether such a high protein diet
400 would be plausible given a likely 'protein ceiling' that would physiologically limit the proportion of
401 meat in the diet. In contemporary AMH, this limit is thought to be about 35% of energy intake
402 (Hardy et al., 2022), which would make a significant carbohydrate component from plant foods
403 essential (Fiorenza et al., 2015; Hardy et al., 2022; Hardy et al., 2015; Hockett, 2012). However, the
404 level of this 'protein ceiling' has been questioned even for contemporary AMH (Klement, 2022). For
405 example, contemporary Arctic hunter-gatherers obtain a remarkably low percentage of energy from
406 carbohydrates (Ströhle and Hahn, 2011) although they have access to extensive marine mammal fat
407 to complement the diet that would have been unavailable to most Neanderthals (Hardy et al., 2022).
408 Anecdotal evidence points to strong plasticity in the metabolic use of different energy substrates
409 (glucose, ketones) and adaptability to the proportion of carbohydrate in the diet in recent humans
410 (Klement, 2022), although it remains unknown how this potential varies across the life course and,
411 critically, during pregnancy and infancy where efficient energy transfer from mother to infant is
412 essential (Hockett, 2012). There is clear genetic evidence for metabolic adaptation in contemporary
413 Arctic human populations consuming diets high in animal products (Clemente et al., 2014; Fumagalli
414 et al., 2015; Moltke et al., 2014), so the possibility of similar genetic adaptations to a low
415 carbohydrate diet in Neanderthals cannot be excluded. Finally, while limits to protein consumption
416 may have existed, at least part of the remaining energy requirements could be met by the

417 consumption of animal fat, bone marrow, and contents of the digestive tract of prey (Buck and
418 Stringer, 2014; Klement, 2022), and extensive processing of animal bones for marrow extraction
419 would support the use of these resources (e.g., Blasco and Fernández Peris, 2012; Vettese et al.,
420 2022).

421

422 In terms of empirical evidence for Neanderthal diets, the analysis of starch grains, plant remains and
423 ancient DNA trapped in dental calculus (mineralised plaque) points to the incorporation of a wide
424 range of plant foods into the Neanderthal diet across their geographical range, including date palm,
425 wild grains, tubers and mushrooms (Henry et al., 2011, 2014; Power et al., 2018; Weyrich et al.,
426 2017). This has been supported by recent reports of charred remains of pounded pulses and wild
427 grains mixed into a kind of paste and cooked from Neanderthal contexts at Shanidar Cave, Iraqi
428 Kurdistan, around 75 kya (Kabukcu et al., 2022). Dental macrowear and microwear analysis support
429 high meat consumption but point to geographical variation in the consumption of plant foods, with
430 greater reliance on plants in more southerly and temperate parts of the Neanderthal range (El
431 Zaatari et al., 2011; Fiorenza et al., 2011). Indeed, clear geographic variation in diet associated with
432 palaeoecology, with greater meat consumption in cold-steppe environments where plant foods
433 were scarcer, has been documented through dental macro- (Fiorenza, 2015; Fiorenza et al., 2011)
434 and microwear (El Zaatari et al., 2011; Estalrich et al., 2017; Pérez-Pérez et al., 2003; Williams et al.,
435 2018) and among individuals from the same site in relation to age-at-death (Williams et al., 2018). In
436 support of a carbohydrate component to the diet, recent work on the Neanderthal microbiome
437 indicates starch consumption (Fellows Yates et al., 2021). In contrast, the selective sweep on
438 increased copy number of the salivary amylase genes (*AMY1*) in modern humans postdates the split
439 from the Neanderthal lineage, imply AMH adapted to carbohydrate-rich diets since we and
440 Neanderthals last shared a common ancestor (Inchley et al., 2016). The weight of the evidence
441 suggests that while Neanderthals likely did eat a high proportion of animal products (meat, marrow,
442 fat etc.) (Jaouen et al., 2019), plant remains played an important role in the diet (Hardy, 2022).

443

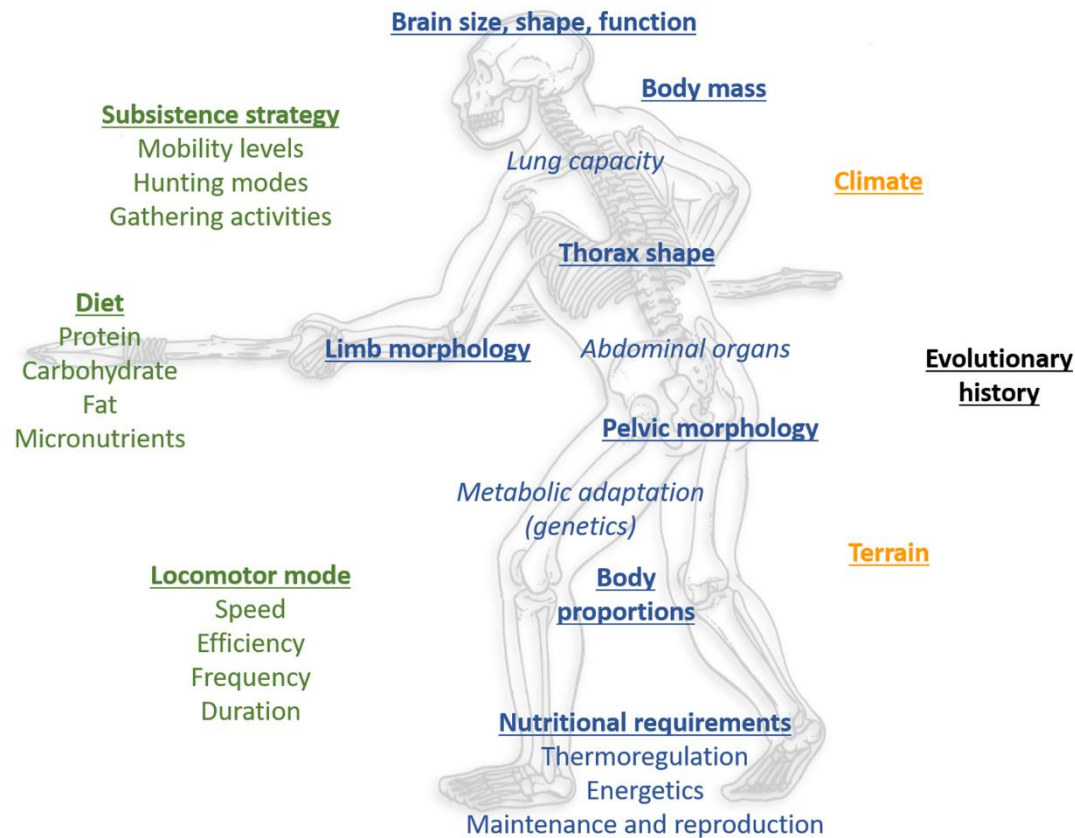
444

445 **Interpreting Neanderthal phenotype**

446

447 How do we then distinguish between the various explanations for Neanderthal morphology and by
448 implication, aspects of their physiology and behaviour (Figure 4)? This is challenging, not least
449 because we might expect these different factors – diet, activity, behaviour, terrain, climate,
450 evolutionary history – to interact in their impacts upon an integrated Neanderthal biology. In trying
451 to explain characters such as the broad, stocky physique and bell-shaped ribcage there is a tendency
452 to focus on a single explanation or individual traits in relative isolation, while a more integrated
453 approach considering energy requirements, diet, thermoregulation, behaviour, environment and
454 evolutionary history may ultimately hold the key in helping to explain Neanderthal biology. While
455 recognising that no human populations alive today are perfect models for Neanderthals, the
456 substantial variation within and between human populations may nonetheless provide considerable
457 opportunities to investigate the relationships between various aspects of behaviour, morphology
458 and physiology, particularly if we look to contemporary athletes who parallel the likely active
459 lifestyles of our evolutionary predecessors (Longman et al., 2020). In doing so, not only will we have
460 an opportunity to understand the integration and evolution of physiological, behavioural and
461 anatomical characteristics in our lineage, but new insights into similar variation within our species
462 may also be achieved as we strive to better understand the integrated nature of our biology.

463



464

465 Figure 4. Summary of the aspects of behaviour (green) and the environment (orange) proposed to
 466 explain anatomical and physiological traits (blue) among Neanderthals. These factors are likely to be
 467 strongly interrelated, and evolutionary history (black) likely also plays an important role, suggesting
 468 a more holistic model is needed to fully understand the Neanderthal phenotype. Neanderthal figure
 469 after Holliday (1997b).

470

471

472 **Implications for understanding modern human physiology and its evolution**

473

474 This brief overview of what we can infer and/or hypothesise regarding Neanderthal physiology and
 475 metabolism demonstrates a number of ways in which exploring Neanderthal biology highlights some
 476 of the gaps in our understanding of modern human physiology, and offers insights into the
 477 evolutionary origins of traits in both species. Morphology, metabolism, behaviour and physiology

478 must be intimately intertwined, but this review highlights some of the deficits in our understanding
479 of these relationships. In particular, the link between the morphology of the gut, pelvis and trunk,
480 and how these characteristics in turn relate to diet, metabolism, and physiological performance are
481 not well elucidated in humans, and so our ability to interpret Neanderthal morphology is held back.
482 Improving our understanding in this regard would not only allow us to gain deeper insights into
483 Neanderthal lifestyles and adaptations, but would permit us to understand variation in
484 contemporary human physiological function and activity. The limitations in our understanding of
485 human protein digestion and metabolism highlighted by the discussion of Neanderthal biology have
486 wider implications for dietary recommendations for the general population, and how these might
487 vary on an individual or population scale, or across different sectors according to age or sex, for
488 example. In the context of elite sports there may be implications for the optimisation of training and
489 diet plans in relation to individual physique and biology, or matching athletes to particular sports in
490 which they are likely to excel. Ultimately, there are evolutionary questions regarding human
491 variation and the origins of morphological, metabolic and physiological characteristics that we will
492 be able to interpret better in light of endeavours to reveal links between these various features
493 within and across contemporary populations, contributing to an understanding of who and what we
494 are as a species.

495

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503

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955 **Figure captions**

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957 Figure 1: Map of Eurasia showing the extent of the known Neanderthal range (modified from
958 https://commons.wikimedia.org/wiki/File:Range_of_Neanderthals.png, under CC BY-SA 3.0).

959

960 Figure 2: Key differences between Neanderthals and anatomically modern humans in their skeletal
961 biology (reproduced with permission from Reilly et al., 2022, Figure 1)

962

963 Figure 3: Characteristics of anatomically modern humans, some shared with other members of the
964 genus *Homo*, that are proposed adaptations to endurance running, based on Bramble and
965 Lieberman (2004, Table 1). Traits are labelled in black, and their inferred function in grey text. Image
966 based on Ryan Hoyme (massagenerds) - [https://pixabay.com/en/muscles-skeleton-half-body-](https://pixabay.com/en/muscles-skeleton-half-body-2277447/)
967 [2277447/](https://pixabay.com/en/muscles-skeleton-half-body-2277447/) archive copy, CC0, <https://commons.wikimedia.org/w/index.php?curid=74822435>.

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969 Figure 4. Summary of the aspects of behaviour (green) and the environment (orange) proposed to
970 explain anatomical and physiological traits (blue) among Neanderthals. These factors are likely to be
971 strongly interrelated, and evolutionary history (black) likely also plays an important role, suggesting
972 a more holistic model is needed to fully understand the Neanderthal phenotype. Neanderthal figure
973 after Holliday (1997b).