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Postcranial evidence from early *Homo* from Dmanisi, Georgia

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The Plio-Pleistocene site of Dmanisi, Georgia, has yielded a rich fossil and archaeological record documenting an early presence of the genus *Homo* outside Africa. Although the craniomandibular morphology of early *Homo* is well known as a result of finds from Dmanisi and African localities, data about its postcranial morphology are still relatively scarce. Here we describe newly excavated postcranial material from Dmanisi comprising a partial skeleton of an adolescent individual, associated with skull D2700/D2735, and the remains from three adult individuals. This material shows that the postcranial anatomy of the Dmanisi hominins has a surprising mosaic of primitive and derived features. The primitive features include a small body size, a low encephalization quotient and absence of humeral torsion; the derived features include modern-human-like body proportions and lower limb morphology indicative of the capability for long-distance travel. Thus, the earliest known hominins to have lived outside of Africa in the temperate zones of Eurasia did not yet display the full set of derived skeletal features.

Since 1991 hominin remains have been recovered from excavation blocks 1 and 2 at Dmanisi, Georgia. Three skulls (D2282/D211, D2700/D2735 and D3444/D3900), one cranium (D2280) and one mandible (D2600) have been described earlier[1–7]. The well-preserved postcranial remains recovered from block 2 provide an insight into previously unknown aspects of early *Homo* morphology and also offer a new comparative perspective on key elements of the postcranial skeleton of the Nariokotome KNM-WT15000 subadult specimen[8] and of *Homo floresiensis*[9].

Stratigraphical context

The geological age of the bone- and artefact-bearing deposits at Dmanisi is approximately 1.77 million years (Myr)[10]. New palaeomagnetic analyses of block 2 deposits are fully concordant with the initial stratigraphical and palaeomagnetic studies of block 1 (Supplementary Information 1). Consideration of the overall mammalian fauna places the site close to the Plio-Pleistocene boundary and shows highest palaeozoogeographical similarity with the chronologically contemporaneous Late Villafranchian of Western Europe (Supplementary Information 2 and 3). Palaeoecological studies point to a remarkable variation in relief, humidity and vegetational character. The presence of fresh water and a variety of ecotones with different vegetal and animal resources nearby made Dmanisi an attractive locale for hominins (Supplementary Information 2–4). Analysis of the taphonomic signature of mammalian remains indicates that hominins were involved in meat acquisition, and that they had early access to carcasses, which suggests hunting or power scavenging. Carnivores were also active at the site, but did not damage bone to the degree found in many hyaena dens (Supplementary Information 5).

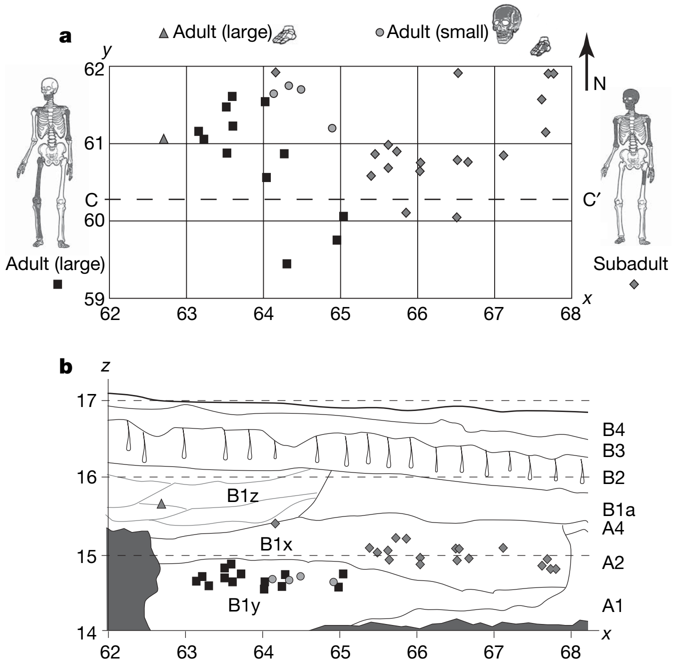

Figure 1 | Stratigraphy of the Dmanisi postcranial hominin remains recovered from block 2. a, Vertical projection (x–y excavation squares are 1×1 m; *in-situ* articulated cervical vertebrae D2673/D2674 are denoted by the double diamond). **b**, Lateral projection along y axis (profile section taken along C–C′) and z axis (metres above zero level reference, see also Supplementary Fig. 1).

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The new hominin skeletal elements from Dmanisi can be assigned to a minimum of four individuals: one adolescent and three adults (Figs 1 and 2). The postcranial remains of the adolescent individual are associated with skull D2700/D2735 (ref. 3). Attribution of all adolescent remains to one individual is based on their close stratigraphical proximity within layer B1x (Fig. 1) and equivalent developmental stages of cranial and postcranial elements (Supplementary Table 3). The spatial distribution pattern of these elements, their uniform stage 0/1 taphonomic condition[11], as well as the partial laminated infilling of the D2700 and D3444 cranial vaults[7], indicate short-distance, low-energy dispersal followed by rapid burial (Supplementary Information 1).

Postcranial remains of three adult individuals, found in layer B1y, exhibit virtually no stratigraphical overlap with the adolescent remains (Fig. 1). These elements are provisionally attributed to one large and two small individuals. The large adult is represented by various elements of the appendicular skeleton. The right femur, tibia and patella exhibit fit in the knee joint, and the left talus, when mirrored to the right side, implies anatomical fit with the tibia. These postcranial remains are probably associated with the large mandible D2600 (ref. 4) found nearby in the same stratigraphical layer (Fig. 1 and Supplementary Fig. 1). Postcranial elements of one smaller adult individual comprise a right medial cuneiform and anatomically associated metatarsal I, and are presumably associated with the small skull D3444/D3900 (refs 5, 7) found nearby. A third adult individual is currently represented by a single metatarsal II found at a higher stratigraphical position (layer B1z; see Fig. 1). Measurements are provided in Table 1, Fig. 3 and Supplementary Information 7.

Upper limbs

D4166 is the lateral part of an adult right scapula comprising the glenoid cavity, and exhibiting some damage across the distal part of the coracoid process. The glenoid cavity is more cranially oriented relative to the midaxillary border than in modern humans, and thus closer to the condition found in australopiths (Sts7 and AL288-1)[12,13] and African great apes. The narrow glenocoracoid angle, the relatively short coracoid process, and the high width-to-length ratio of the coracoid process are outside the range of variation found in modern humans, and are similar to great apes[14], whereas the glenoid orientation relative to the spine and the breadth-to-width ratio of the spine are at the lower end of modern-human variation and similar to KNM-WT15000. D4161 and D4162 are left and right adult

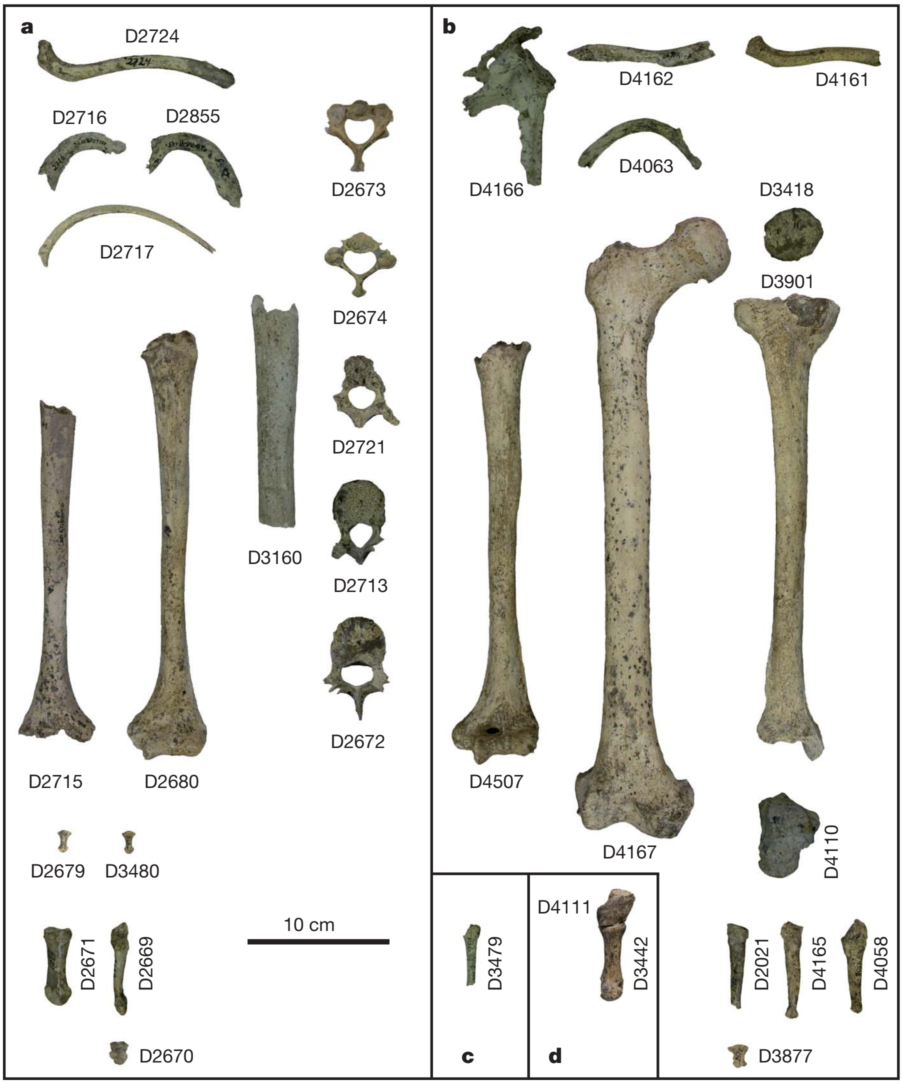

Figure 2 | Dmanisi postcranial elements. **a**, Remains of subadult individual. D2724, left clavicle; D2716/D2855, right/left first rib; D2717, eleventh rib; D2673/D2674/D2721/D2713/D2672, vertebrae C2/C3/Th3/Th10/L1; D2715/D2680, right/left humerus; D3160, left femur; D2679/D3480, distal phalanges of hand; D2671/D2669, right metatarsal I/IV; D2670, first distal phalange of right foot. **b**, Remains of large adult individual. D4166, right scapula; D4162/D4161, right/left clavicles; D4063, right second rib; D4507, left humerus; D4167, right femur; D3418, right patella; D3901, right tibia; D4110, left talus; D2021/D4165, right metatarsals III/IV; D4508, left metatarsal V; D3877, distal phalange of foot. **c**, **d**, Remains of small adult individuals. D3479, right metatarsal III; D4111, right medial cuneiform; D3442, right metatarsal I.

clavicles, respectively. Both elements lack their sternal and acromial ends. D2724 is an almost complete subadult left clavicle with some damage at the epiphyses. The shaft is comparatively short, similar to Chk-B-2-81 (Zhoukoudian *Homo erectus*)[15] and OH48 (*Homo habilis*)[16], but within the range of variation displayed by subadult modern humans. In their mid-shaft and conoid tubercular cross-sectional shape, all Dmanisi clavicles are more similar to modern humans and Chk-B-2-81/OH48 than to KNM-WT15000, which has a greater antero-posterior than supero-inferior diameter. D2680 and D2715 are left and right subadult humeri; D4507 is a left adult humerus. In both individuals, the humeral shaft is almost straight, and the position of the lateral epicondyle in relation to the lateral condyle is comparatively high. This is different compared with the condition found in modern humans, but similar to Plio-Pleistocene hominins[17] and African great apes. Humeral torsion in the Dmanisi sample is virtually absent, similar to australopiths (AL288-1, Sts7, KNM-ER739)[18] and *H. floresiensis*[19] (LB1), whereas the KNM-WT15000 humeri are at the lower end of variation of modern-human-like degrees of torsion.

Axial skeleton

The vertebral column of the subadult individual is represented by five elements: D2673 (cervical 2 (C2), axis), D2674 (C3), D2721 (thoracic ~3 (Th3)), D2713 (thoracic ~10 (Th10)) and D2672 (lumbar 1 (L1)). In C2, the superior articular process is sloping downwards mediolaterally, as in the great apes and australopiths, but the spinal process is short and narrow, similar to the condition found in modern humans and australopiths. Canal shapes of all vertebrae are wider transversally than dorso-ventrally, similar to AL333-101, KNM-WT15000 and modern humans. Zygapophyseal joint orientation of C3, Th10 and L1 is like that in modern humans. The centra of Th10 and L1 are transversally extended; T10 exhibits anterior wedging, whereas L1 exhibits slight posterior wedging.

Lower limbs

The adult right femur, tibia and patella constitute the most complete lower limb of early *Homo* recovered so far. D4167 is a complete right femur with a well-developed linea aspera. The shaft is markedly more robust than that of KNM-ER1481a[20] (early *Homo*). The neck index is similar to australopiths and KNM-WT15000, but lower than in modern humans. As in all hominins[21], the greater trochanter is less elevated than the head but is laterally prominent. In keeping with the low degree of anteversion (femoral torsion), the lesser trochanter is not carried far towards the medial margin of the shaft[22]. Like Asian and African *H. erectus*, the Dmanisi femur has a narrow medullary canal[21] in comparison to modern humans. The shaft is straight in anterior view and displays the valgus orientation characteristic for hominins. The distal bicondylar angle is within the range of variation of australopiths and early *Homo*[23], and at the upper extreme of modern human variation. D3418 is a right patella. The medial surface is larger than the lateral surface, which is unusual in modern humans. The mediolateral breadth is slightly larger than that of the left patella SKX 1084 (ref. 24) from Swartkrans Member 2. D3901 is the first complete fossil hominin tibia. It is comparatively robust; the proximal and distal joint surfaces and the malleolus are large relative to diaphyseal length (Fig. 3a), but mid-shaft proportions are like those of early *Homo* (KNM-ER803b, KNM-ER741)[25,26]. D3901 is similar to modern human tibiae in its degree of torsion, but clearly different in its degree of inclination. This latter feature is pronounced in humans, but not in great apes.

Table 1 | Postcranial dimensions of the Dmanisi hominins

Measurements	Australopiths	Earliest *Homo*	Dmanisi	KNM-WT15000	Modern humans
Shoulder girdle					
Olecranon orientation relative to midaxillary border (M17) (°)	115.0–116.0†	–	129.0	*127.0*	133.8–154.0
Glenocoracoid angle (°)	–	–	55.0	*59.5*	60.0–94.5
Clavicular length (M1) (mm)	–	149.4‡	137.3 (L), 135.6 (R), *123.2*	*130.5*	113.0–159.0, *113.0–139.0*
Humerus					
Length (M1) (mm)	226.0–235.0§	–	295.0, *282.2*	*319.0*	263.0–341.0, *255.0–334.0*
Mid-shaft a–p diameter (mm)	19.0	–	37.1, *17.1 (L), 16.8 (R)*	*19.9*	16.5–36.0, *12.5–24.3*
Mid-shaft m–l diameter (mm)	15.0	–	34.8, *14.3 (L), 14.7 (R)*	*16.7*	11.5–24.5, *13.3–31.4*
Torsion (M18) (°)	111.0–130.0‖	–	110.0, *104.0*	*126.0*	134.9–180.0, *138.2–160.7*
Vertebrae					
C2 anterior angle of superior articular process (°)	107.0–120.0¶	–	*111.0*	–	*129.1–147.2*
C2/C3 zygapophyseal joint angle (°)	–	–	*62.5*	–	*62.0–85.0*
Th10 centrum area (M4*M7) (mm^2)	–	–	*692.2*	–	*601.1–958.6*
L1 centrum area (M4*M7) (mm^2)	–	–	*777.8*	*803.4*	*706.3–1,288.9*
Femur					
Length (M1) (mm)	280.0#	401.0–396.0☆	386.0	*432.0*	337.0–434.0
Head diameter (M19) (mm)	27.9–39.4**	40.0–42.0☆	40.0	*46.0*	42.7–55.1
Mid-shaft a–p diameter (M6) (mm)	22.0#	27.7–28.8☆	26.5	*24.5*	29.1–34.7
Mid-shaft m–l diameter (M7) (mm)	21.0#	26.4–25.6☆	22.2	*24.3*	26.1–29.9
Medial condylar breadth (M21c) (mm)	19.3–22.3††	20.7–21☆	24.2	–	27.6–40.3
Lateral condylar breadth (M21e) (mm)	17.9–22.1††	19.2–25.5☆	23.3	–	24.2–32.9
Bicondylar angle (M30) (°)	75.0–81.0‡‡	77.0–80.0☆	81.5	*80.0*	76.0–88.0
Tibia					
Length (M1a) (mm)	–	–	306.0	*380*	290.0–374.0
Mid-shaft a–p diameter (M8) (mm)	–	22.5–31.0§§	27.0	*24.5*	25.8–42.3
Mid-shaft m–l diameter (M9) (mm)	–	14.6–23.6§§	18.0	*20.4*	15.5–24.6
Angle of inclination (M13) (°)	–	–	82.0	–	89.1–111.7
Foot					
Neck angle of talus (M16) (°)	32.3‖‖	33.5¶¶	26.0	–	12.0–31.0
Estimates*					
Stature (cm)	110.0–151.0 (ref. 50)	125.0–157.0 (ref. 50)	144.9–166.2	*150.5–169.1* (ref. 42)	–
Body mass (kg)	29.0–49.0 (ref. 50)	32.0–52.0 (ref. 50)	40.0–50.0	*45.5–70.6* (ref. 42)	–
Encephalization quotient	2.4–3.1 (ref. 50)	3.1 (ref. 50)	2.57–3.13	*2.71–3.78*	6.3

Measurement ranges were used for australopiths and modern humans. Data for subadults are in italic font. a–p, antero-posterior; m–l, mediolateral. For measurement codes (M1, M7, and so on) see ref. 69 of Supplementary Information.

* See Supplementary Table 6 for details on estimation procedures. †Sts7, AL288-1. ‡OH48. §AL288-1, Bou-VP-12/1. ‖AL288-1, ER739, Sts7, Omo119. ¶AL333-101, SK-854. #AL288-1. ☆KNM-ER1481, KNM-ER1472. **AL288-1, AL333-4. ††AL129, AL333-4, Sts34, TM1513. ‡‡AL288-1, AL129-1a, AL333-4, AL333w-56, Sts34, TM1513, ER993. §§OH35a, ER813a, ER741. ‖‖AL288-1, TM1517, ER1476a, ER813, ER1464, Stw573. ¶¶OH8.

Foot bones

D4110 is a well-preserved left talus. The neck is stout and expanded transversely but elongated compared to modern humans. The neck (horizontal) angle is small and similar to modern humans[27]. The medial tubercle is strong and projecting, and the groove for the tendon of flexor hallucis longus is deep. This groove has a slightly oblique orientation, which is similar to great apes, whereas humans exhibit a more vertical orientation[28]. D2671 and D3442 are subadult and adult right first metatarsals, respectively, with lengths at the lower end of modern human variation and elevated robusticity indices. The morphology of the head deviates from that known from apes and humans. It is spherical and exhibits a narrowing of the dorsal breadth of the articular surface[29]. Head torsion is in the range of variation of subadult and adult modern humans and of OH8 (*H. habilis*)[30]. Two adult metatarsals III (D2021 and D3479) have a straight shaft, exhibit a high degree of torsion and have a dorso-ventrally elongated cross-sectional shape, as in modern humans. Metatarsals IV (adult D4165 and subadult D2669) exhibit an elevated degree of torsion and dorso-ventral elongation. Adult metatarsal V (D4508) is short and at the lower end of modern human variation for its mid-shaft dimensions.

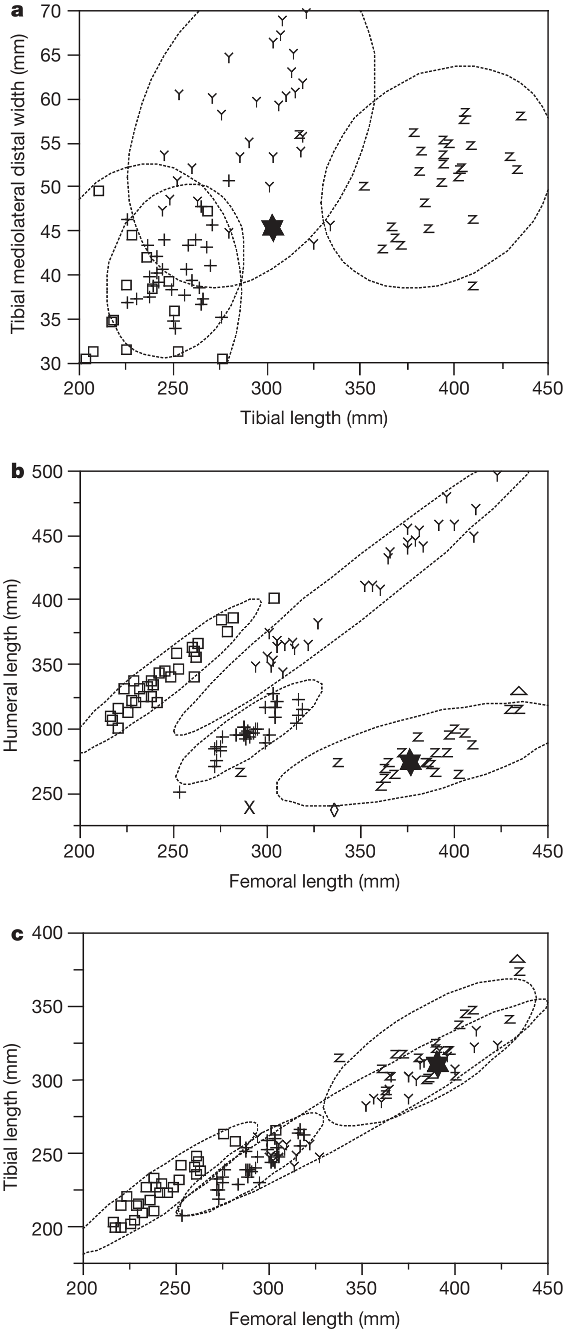

Figure 3 | Long-bone shape and proportions. **a**, Tibial mediolateral distal width versus maximum length. **b**, Humeral versus femoral length. **c**, Tibial versus femoral length. Stars, Dmanisi *Homo*; X, AL288-1 (*Australopithecus afarensis*); diamond, BOU-VP-12/1; triangle, KNM-WT15000 (*H. erectus*); Z, recent *Homo sapiens*; plus signs, *Pan troglodytes*; Y, *Gorilla gorilla*; squares, *Pongo pygmaeus*.

Evolutionary and functional context

The postcranial morphology of the australopiths is best documented by the AL288-1 specimen[31], indicating that their stature was small (105 cm) and their limb proportions between those of great apes and modern humans, suggesting terrestrial bipedalism with retained arboreal locomotor capabilities. Contrastingly, the postcranial morphology of earliest *Homo* (cf. *H. habilis*) is known from only a few fragmentary specimens (for example, OH35, OH62, KNM-ER3735 (refs 32–35)) dated between 1.75- and 1.9-Myr ago[36,37], such that inferences regarding the evolution of stature and limb proportions in this genus are a matter of ongoing debate[38–40]. The first well-documented evidence for the postcranium of genus *Homo* comes from the KNM-WT15000 specimen, dated to approximately 1.55 Myr ago, the body proportions and stature of which are modern in almost every aspect[8]. Information about the transition from australopith-like to modern-human-like postcranial morphologies is thus rather limited, and the Dmanisi postcranial material fills significant gaps in our knowledge about this critical period of hominin evolution.

The presence of anatomically matching proximal and distal lower limb bones (D4167 and D3901) in the Dmanisi sample and the likely association of these elements with humerus D4507 can be used to infer stature and limb proportions. Stature and body mass of the Dmanisi individuals calculated from various independent long bone measurements yield estimates between 145–166 cm and 40–50 kg, respectively (Table 1 and Supplementary Information 8). Their small stature might be interpreted in two different, but non-exclusive, ways. On the one hand, it might represent a plesiomorphic character shared with earliest *Homo* (cf. *H. habilis*) (125–157 cm and 32–52 kg[41]), whereas the KNM-WT15000 specimen appears to be derived in this respect (150.5–169.1 cm and 45.5–70.6 kg)[42]. On the other hand, differences in stature between the Dmanisi and KNM-WT15000 hominins might reflect adaptation to different palaeo-ecological contexts. Limb proportions of the Dmanisi hominins, measured by femoral/tibial and humeral/femoral ratios (Fig. 3b, c and Table 1), were similar to those of modern humans, but also to those of earliest African *Homo* and to the BOU-VP-12/1 specimen dated to 2.5 Myr ago[43]. Absolute hindlimb length of the Dmanisi hominins is greater than in australopiths and close to that of later *Homo* including modern humans. This may reflect selection for improved locomotor energy efficiency, as the cost of transport is inversely proportional to hindlimb length for terrestrial animals including bipeds[44].

Cranial capacities (roughly equivalent to brain volume) for the Dmanisi individuals vary from 600 to 775 cm^3 (refs 2, 3, 7). These values overlap with *H. habilis* ($614 \pm 66\ \mathrm{cm}^3$; $n = 6$)[45], but are more than one standard deviation below the mean for *H. erectus* ($904 \pm 100\ \mathrm{cm}^3$; $n = 13$)[46]. Combining cranial and postcranial dimensions, the encephalization quotient for the Dmanisi individuals is in the range of 2.6 to 3.1 (Table 1 and Supplementary Table 6), which is at the lower end of estimates for KNM-WT15000 (2.7–3.8) and more comparable to *H. habilis* (3.1) and australopiths (2.4–3.1).

Using modern human dental and postcranial developmental scores, the age difference between the Dmanisi and KNM-WT15000 specimens is around 2 yr (assuming individual ages of 11–13 and 8–10 yr, respectively), so these specimens are broadly comparable to each other. Overall vertebral morphology indicates that the Dmanisi spine was more similar to that of early *H. erectus* and modern humans than to australopiths. Vertebral wedging is indicative of lumbar lordosis; zygapophyseal joint orientation suggests expanded ranges of spinal flexion; and the relatively large vertebral cross-sectional areas are indicative of resistance to increased compressive loads characteristic of running and long-range walking[47].

Humeral torsion is an important variable that influences orientation and ranges of movement of the upper limb relative to the trunk. In modern humans, the high degree of torsion is seen as a compensation for the more dorsal position of the scapula[18]. The low degree of torsion in the Dmanisi sample could thus indicate a habitually more abducted/supine orientation of the arm, a more lateral position of the shoulder girdle, and also a diverse range of arm movement. Reduced torsion in the throwing arm of athletes requiring high upper limb mobility (external rotation)[48] suggests developmental plasticity, but because this feature is not lateralized in the Dmanisi subadult individual, it might be interpreted as part of a plesiomorphic configuration of the upper body that also includes a more cranial orientation of the glenoid cavity of the scapula, a short coracoid process and a narrow glenocoracoid angle. Following this line of argument, the Dmanisi hominins would have had a more australopith-like than human-like upper limb morphology[49], and absence of humeral torsion in *H. floresiensis*[9] would provide support for the hypothesis of long-term continuity of this plesiomorphic trait in *Homo*.

Preservation in the Dmanisi remains of lower limb elements from the femur down to the metatarsals permits reconstruction of the positioning and orientation of the foot relative to the walking direction. The tibia exhibits slight medial torsion, and the talar neck angle is wide. This combination results in a more medial orientation of the foot, and a more equal load distribution on all rays than in modern humans. Although this configuration probably represents the plesiomorphic condition, various features of the Dmanisi foot are similar to modern humans and thus clearly derived: metatarsal torsion indicates the presence of a transverse arch; the wide base of the first metatarsal suggests a strong plantar ligament associated with a well-developed longitudinal arch[29]; and the flat proximal articular surface of the first metatarsal indicates that the hallux had an adducted position.

The following preliminary conclusions can be drawn: the morphology of the upper and lower limbs from Dmanisi exhibits a mosaic of traits reflecting both selection for improved terrestrial locomotor performance and the retention of primitive characters absent in later hominins (Supplementary Table 8). The length and morphology of the hindlimb is essentially modern, and the presence of an adducted hallux and plantar arch indicate that the salient aspects of performance in the leg and foot, such as biomechanical efficiency during long-range walking and energy storage/return during running, were equivalent to modern humans. However, plesiomorphic features such as a more medial orientation of the foot, absence of humeral torsion, small body size and low encephalization quotient suggest that the Dmanisi hominins are postcranially largely comparable to earliest *Homo* (cf. *H. habilis*). Hence, the first hominin species currently known from outside Africa did not possess the full suite of derived locomotor traits apparent in African *H. erectus* and later hominins.

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