



# UNIVERSITAT DE BARCELONA

## Modelización biomecánica de la locomoción bípeda en humanos y homínidos

Gerard Saborit González

**ADVERTIMENT.** La consulta d'aquesta tesi queda condicionada a l'acceptació de les següents condicions d'ús: La difusió d'aquesta tesi per mitjà del servei TDX ([www.tdx.cat](http://www.tdx.cat)) i a través del Dipòsit Digital de la UB ([diposit.ub.edu](http://diposit.ub.edu)) ha estat autoritzada pels titulars dels drets de propietat intel·lectual únicament per a usos privats emmarcats en activitats d'investigació i docència. No s'autoritza la seva reproducció amb finalitats de lucre ni la seva difusió i posada a disposició des d'un lloc aliè al servei TDX ni al Dipòsit Digital de la UB. No s'autoritza la presentació del seu contingut en una finestra o marc aliè a TDX o al Dipòsit Digital de la UB (framing). Aquesta reserva de drets afecta tant al resum de presentació de la tesi com als seus continguts. En la utilització o cita de parts de la tesi és obligat indicar el nom de la persona autora.

**ADVERTENCIA.** La consulta de esta tesis queda condicionada a la aceptación de las siguientes condiciones de uso: La difusión de esta tesis por medio del servicio TDR ([www.tdx.cat](http://www.tdx.cat)) y a través del Repositorio Digital de la UB ([diposit.ub.edu](http://diposit.ub.edu)) ha sido autorizada por los titulares de los derechos de propiedad intelectual únicamente para usos privados enmarcados en actividades de investigación y docencia. No se autoriza su reproducción con finalidades de lucro ni su difusión y puesta a disposición desde un sitio ajeno al servicio TDR o al Repositorio Digital de la UB. No se autoriza la presentación de su contenido en una ventana o marco ajeno a TDR o al Repositorio Digital de la UB (framing). Esta reserva de derechos afecta tanto al resumen de presentación de la tesis como a sus contenidos. En la utilización o cita de partes de la tesis es obligado indicar el nombre de la persona autora.

**WARNING.** On having consulted this thesis you're accepting the following use conditions: Spreading this thesis by the TDX ([www.tdx.cat](http://www.tdx.cat)) service and by the UB Digital Repository ([diposit.ub.edu](http://diposit.ub.edu)) has been authorized by the titular of the intellectual property rights only for private uses placed in investigation and teaching activities. Reproduction with lucrative aims is not authorized nor its spreading and availability from a site foreign to the TDX service or to the UB Digital Repository. Introducing its content in a window or frame foreign to the TDX service or to the UB Digital Repository is not authorized (framing). Those rights affect to the presentation summary of the thesis as well as to its contents. In the using or citation of parts of the thesis it's obliged to indicate the name of the author.

## A Dynamic Analysis of Middle Pleistocene human walking gait adjustment and control

GERARD SABORIT (1), ALESSANDRO MONDANARO (2,3), MARINA MELCHIONNA (2), CARMELA SERIO (2), FRANCESCO CAROTENUTO (2), STEFANO TAVANI (2), MARIA MODAFFERI (2), ADOLFO PANARELLO (4), PAOLO MIETTO (5), PASQUALE RAIA (2) & ADRIÀ CASINOS (1)

### ABSTRACT

Understanding the evolution of bipedal locomotion in humans is of paramount importance to paleoanthropologists. Such endeavor requires well-preserved dynamic evidence of fossil human locomotion we are short of. Physical models of modern human locomotion predict individuals would perform voluntary step length adjustment as a function of slope gradient in order to minimize the energetic cost of locomotion while maintaining balance and reasonably comfortable gait. The famous Roccamonfina volcano “Devil’s trails”, which are Middle Pleistocene *Homo* fossilized trackways, provide unique opportunity to validate such predictions for fossil human individuals. We studied the best-preserved Roccamonfina Devil’s trail to ascertain the dynamic behavior of the individual who left the trackway. We found Roccamonfina’s individual moved in a way which is dynamically equivalent to modern humans, adjusting gait as to minimize energy expenditure. We derived body mass and stature estimates for such individual, which fit perfectly with previously published figures for Middle Pleistocene hominins outside Africa.

KEY WORDS: *Homo heidelbergensis*, *Roccamonfina*, *Devil’s trails*, human locomotion

### INTRODUCTION

Mammal tracks represent some 20% of the total fossil tetrapod trail record (LOCKLEY *et alii*, 2007). Among them, the tracks of hominins stand out for being at one time among the most important and rarest (LOCKLEY *et alii*, 2008). LOCKLEY *et alii* (2008) documented 63 different hominin footprint sites, extending from the Pliocene (Laetoli, 3.7 MA) to the Holocene (about 1,000 years BP). Most tracks were found

in open air conditions, although a few occur within caves or other closed environments (BENNETT & MORSE, 2014; LOCKLEY *et alii*, 2008; PANARELLO, 2016). Among the former, the well-known Roccamonfina’s “Devil’s trails” (Caserta, Southern Italy) stands out for the exceptionally rich and well-preserved evidence, and for being laid on a sloping irregular surface, which gives the unique opportunity to look at a fossil hominin gait adjustment along a single trackway (MIETTO *et alii*, 2003). As of today, three different fossil trackways (A, B, and C), associated with other mammalian tracks, have been described at Roccamonfina (AVANZINI *et alii*, 2008; PANARELLO *et alii*, 2017). The “Devil’s trails” were radiometrically dated at 349-350±3 kyr with <sup>40</sup>Ar/<sup>39</sup>Ar method (SANTELLO, 2010; SCAILLET *et alii*, 2008). The footprints were clearly left by individuals belonging to a human species. The dating is consistent with one species in particular, *Homo heidelbergensis* (SCAILLET *et alii*, 2008), although genetic studies trace back the origin of *Homo neanderthalensis* to almost the same period (ENDICOTT *et alii*, 2010). The Roccamonfina footprints were considered the oldest human footprints outside the Africa, until the recent discovery of a human footprint surface at Happisburgh, UK, dated in between ca. 1 and 0.78 Ma (ASHTON *et alii*, 2014). More recently, an enigmatic Miocene footprint set was described in Trachilos (Crete, Greece). However, the track might refer to an unknown late Miocene ape that convergently evolved human-like foot anatomy (GIERLINSKI *et alii*, 2017).

The three Roccamonfina trails descend along a sloping volcanic outcrop at different angles. Specifically, the footprints of the trackway A suggest that the hominin deliberately chose an oblique route cutting avoiding the steepest gradient along the path (AVANZINI *et alii*, 2008; MIETTO *et alii*, 2003). This precious behavioral information allows to expand our knowledge of fossil hominin locomotion, which is the subject matter of this investigation.

Human locomotion is a costly behavior. Humans save energy during walking by exploiting a pendulum-like movement which converts potential to kinetic energy (CAVAGNA *et alii*, 1977). At running, the pendulum system does not work since there is coincidence between the maxima of potential and kinetic energy. Alternatively, a mechanism recovering elastic energy stored in the Achilles tendon and in the sole is exploited (ALEXANDER, 1992). HATALA *et alii* (2016) showed that the arched foot, hence a conceivably similar energy-saving system, was already present in *Homo erectus*. Whatever energy-saving system applies, the labor transfer cannot occur at 100% efficiency,

(1) Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, 08028 Barcelona, Spain. Email: [gsaborit@gmail.com](mailto:gsaborit@gmail.com); [acasinos@ub.edu](mailto:acasinos@ub.edu).

(2) Dipartimento di Scienze della Terra, dell’Ambiente e delle Risorse, Università degli Studi di Napoli Federico II, Via Cinthia, 21, Monte Sant’Angelo, Napoli 80126, Italy. Email: [alessandro.mondanaro@unifi.it](mailto:alessandro.mondanaro@unifi.it); [marina.melchionna@unina.it](mailto:marina.melchionna@unina.it); [karmserio@gmail.com](mailto:karmserio@gmail.com); [francesco.carotenuto@unina.it](mailto:francesco.carotenuto@unina.it); [stefano.tavani@unina.it](mailto:stefano.tavani@unina.it); [m.modafferi@studenti.unina.it](mailto:m.modafferi@studenti.unina.it).

(3) Dipartimento di Scienze della Terra, Università degli studi di Firenze, Via G. La Pira 4, Firenze 50121, Italy. Email: [alessandro.mondanaro@unifi.it](mailto:alessandro.mondanaro@unifi.it).

(4) Laboratorio di Ricerche Storiche e Archeologiche dell’Antichità, Dipartimento di Scienze Umane, Sociali e della Salute, Università degli studi di Cassino e del Lazio Meridionale, Via S. Angelo - Campus Folcara, Cassino 03043, Italy. Email: [info.adolfo.panarello@gmail.com](mailto:info.adolfo.panarello@gmail.com).

(5) Dipartimento di Geoscienze, Università degli Studi di Padova, Via G. Gradenigo 6, Padova 35131, Italy. Email: [paolo.mietto@unipd.it](mailto:paolo.mietto@unipd.it). Corresponding author e-mail: [pasquale.raia@unina.it](mailto:pasquale.raia@unina.it).

and additional energy must be fed into the system at each step. Empirical evidence coming from oxygen consumption experiments indicate that the minimum energetic cost during either walking or running is not achieved by moving on a flat surface, but on a negative slope of minus 10 to minus 20° (being steeper at running) (MARGARIA, 1976; MINETTI *et alii*, 2002; SABORIT & CASINOS, 2015). RUE & KRAMER (2017) demonstrated that these figures, obtained by having human individuals moving over treadmills, are also valid in non-lab (overground) conditions. KRAMER (2010) showed that body mass, sex, and gait cumulatively explain 87% of the variation in the energetic expenditure in gradient walking.

SABORIT & CASINOS (2015) showed that on a downhill slope, humans adjust their walking strategy by either changing the length of the steps or making for a transversal path in order to move along a shallower slope. A single parameter,  $K$ , defined as the ratio of limb to step lengths, has a range of physiologically feasible values in *Homo sapiens*. Within the range of  $K$  exploited by humans, energy consumption rate is minimized, assuming that people voluntarily adjust their gaits to reduce expenditure (ALEXANDER, 1980; 1984; SCHEFFER & LINDSTEDT, 2013). STEUDEL-NUMBERS *et alii* (2007) showed that longer limbs tend to produce lower locomotor expenditure. Unfortunately, though, the relationship between stride and limb lengths is not well understood in fossil hominins, despite its importance to fully understand the evolution of our walking dynamics.

Different papers have been published in the last few years about the energetic cost of locomotion in fossil hominins. Their results are not always coincident. KRAMER & ECK (2000) investigated the locomotion of *Australopithecus afarensis* (based on the proportions of AL 288-1 'Lucy' skeleton) in comparison to a typical modern woman. According to their results, at walking speed Lucy spent less energy than a modern woman, but the preferred transition speed from walking to running in AL 288-1 would occur at a much slower speed. SELLERS *et alii* (2005) estimated the most energy-efficient walking gait for Lucy, by means of a robotic simulation. They concluded that these early hominins were a fully-competent bipeds. However, at comparing *A. afarensis* footprints at Laetoli G (WHITE & SUWA, 1987) with those of modern humans and chimpanzees, RAICHLIN *et alii* (2008) argued it was not possible to ascertain which species the Laetoli hominin locomotion was more similar to. New footprints at Laetoli S were described as biomechanically equivalent to the footprints at Laetoli G, but referred to individuals of different stature and body mass (MASAO *et alii*, 2016).

STEUDEL-NUMBERS (2007) demonstrated that relative limb elongation afforded *Homo erectus* a reduction in energy expenditure of some 50% over AL 288-1. VIDAL-CORDASCO *et alii* (2017) used body mass, femur length, and bi-iliac breadth, to calculate the net and gross cost of locomotion in different extinct hominins. They concluded that *Homo* is not energetically more efficient than *Australopithecus* in terms of locomotion, neither *Homo sapiens* has more efficient (i.e. less expensive) walking as compared to fossil *Homo* species.

Here, we belabored an application of SABORIT & CASINOS' model (2015) which allows to calculate  $K$ , locomotory costs, and to estimate body mass and limb lengths for fossil hominins starting from fossilized trackways. We applied this method to the Roccamonfina's trackway A, in order to

understand how the hominin individual left the footprints, and whether it tried to minimize energy expenditure during the downhill walking. We compared dynamically the Roccamonfina individual to modern *H. sapiens* taking in mind *H. ergaster* and subsequent fossil members of the genus *Homo* possessed proportions similar to those of modern humans (GRUSS, 2007). Specifically, we computed the locomotory costs, and estimated its stature and body mass.

## MATERIAL AND METHODS

We focused on Roccamonfina's trackway A (cf. AVANZINI *et alii*, 2008; MIETTO *et alii*, 2003), which can be divided into three sections separated by two sharp changes in slope. Footprints in this trackway are well-defined, and clearly the hominin was neither running nor having balance issues.

Despite the fact that speed, and thus kinetic energy, has an important role in the mechanical energy analysis of human locomotion, it was shown by SABORIT & CASINOS (2015) that at low and constant speed, as it the case in the Roccamonfina trackway A, the term of kinetic energy is much lower than that of potential energy in calculating overall expenditure. Consequently, we removed the kinetic energy term from the analysis as a first approach.

Measurements were taken directly on the footprints of the central and final section (footprints 11-14 and 21-25; see AVANZINI *et alii*, 2008) to select the best and less controversial consecutive footprints. For each footstep, we took the step length by direct measurement by one of us (AP), and the slope between consecutive footprints on a digital model of the terrain. This three-dimensional digital reconstruction (digital outcrop model, DOM) of trackway A (Fig. 1A) consists of a point cloud produced by means of multi-view stereo-photogrammetry (e.g. FAVALLI *et alii*, 2012; REMONDINO & EL-HAKIM, 2006). The DOM was produced by using the Agisoft Photoscan software package. In detail, 343 photographs were used to build a point cloud of 82057738 points, representing the surface of the exposure hosting the trackway. The point-cloud was scaled and georeferenced using five non co-linear control points, following the pipeline described in TAVANI *et alii* (2016). The area covered by the model was about 46 m<sup>2</sup>, resulting in a resolution of 1.7 point/mm<sup>2</sup>, which increases to 4.5 point/mm<sup>2</sup> along the trackway (Fig 1B).

Slopes between consecutive footprints were retrieved directly from the DOM, to the nearest  $1 \cdot 10^{-2}$  degree. To achieve the best possible precision and to minimize operator induced error, this procedure was run independently by two operators for a total of 5 slope measurements for each footstep. Eventually, we averaged the slopes between consecutive footprints for further analyses. Finally, we transformed trigonometrically the slope values into a vertical displacement  $dy$  and forward displacement  $dx$  components, whose ratio  $dy/dx$  defines the gradient index  $i$ .

The step length ( $\lambda$ ) taken directly on the trackway A, represents the distance between a line perpendicular to heel reference point and its intersection with the opposite contralateral line of progression (WILKINSON & MENZ, 1997).

Besides  $i$  (the gradient) a crucial index in SABORIT & CASINOS' (2015) model is  $K$ . This ratio links to step ( $\lambda$ ) and limb lengths ( $l$ ) through the equation  $K = l/\lambda$ . Limb length



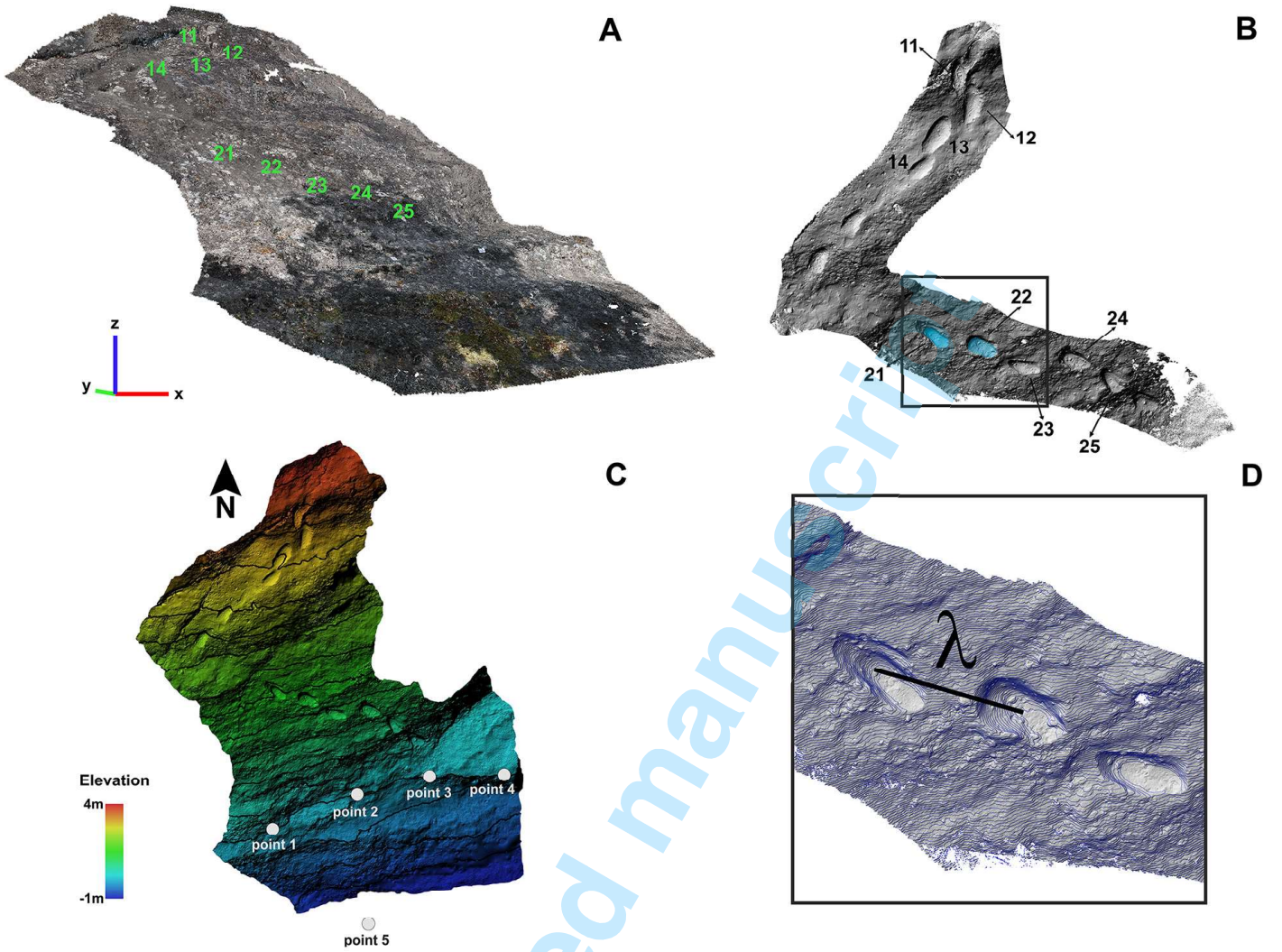


Fig. 1 - Digital outcrop model (DOM) of human footprints. A) The DOM of trackway A, with individual footprints numbered in green. A local coordinate system is used in the model, with the origin set at Latitude 41.33° N, Longitude 14.02° E, Elevation 284 m. B) Footprints in upper view (from the top down). Footprints 21 and 22 are highlighted. C) The Elevation model of trackway A, the reference points placed to produce the DOM are indicated. D) The approach undertaken to calculate the step length  $\lambda$  (here between footprints 21 and 22).

is, plainly, tightly correlated to body size. In turn, body size,  $K$ ,  $i$ , and  $l$  define energy expenditure during locomotion (SABORIT & CASINOS, 2015), according to the equation:

$$mgl \frac{i}{k} \sqrt{\frac{1}{1+i^2}} + mgl \left( 1 - \sqrt{1 - \frac{1}{4k^2}} \right) = 0 \quad (1)$$

Where the first term defines the variation in potential energy spent to move over a gradient for each step, and the second term is the potential energy spent during oscillation of the body center of mass at each step. Both terms are expressed in Joules.

To find the best-fit estimates for body size and limb lengths ( $l$ ) of the Roccamonfina individual, and select the parameter combination minimizing total expenditure, we proceeded as follows:

1. We drew a normal body size distribution of 1000 estimates centered at 66 kg, whereas the corresponding standard deviation was arbitrarily set at one tenth of

the average body size, that is 6.6 kg. The mean of this distribution coincides with the average body mass for Middle Pleistocene humans (RUFF *et alii*, 1997; WILL *et alii*, 2018), whereas the resulting size range spans from some 40 to some 90 kg which is conceivably close to the actual range of human body size variation. Although large, the body size range consistently includes potential effects on body size variation introduced by geography and sexual dimorphism (RUFF *et alii*, 2002).

2. We found the maximum likelihood estimate of  $K$  as follows:

a. Pick a single body size value  $m$  from the distribution of body masses described in point 1, and derive a limb length estimate  $l$  for  $m$  from an allometric equation, produced according to literature data on fossil *Homo* and explained in detail in the supplementary material. In brief, the allometric equation defining the relationship between body size and limb length has a slope of 1.092 and an intercept of 1.928 ( $p < 0.001$ , R-squared = 0.573) (Fig. S1). To take statistical uncertainty into account, we used the 95% confidence interval around this slope estimate (that is

any value taken randomly in between 0.795 and 1.388) to estimate limb lengths (Appendix S1).

b. Find the maximum likelihood estimate of  $K$  ( $K_{fit}$ ) that minimizes the difference between  $l$  and an additional estimate of limb length  $l'$  obtained according to the equation  $K=l'/\lambda$ .

3. Compute the actual limb length  $l_{fit}$  according to the equation  $l_{fit} = K_{fit} * \lambda$ .

4. Compute the energy expenditure over the entire trackway as with equation (1), after removing the body size term ( $mgl$ ) in order to obtain a mass specific (i.e. per  $kg^{-1}$ ) expenditure ("en.by.step"). This equation gives the energy expenditure over one step per unit  $m$  computed starting from  $K$  values fitted in the likelihood function. Since kinetic energy, as well as other energetic costs (i.e. basal costs), was not taken into account, the energy expenditure calculated equals to the potential energy expenditure, which closely approximate the total expenditure.

5. Repeat the procedures in points 2 to 4, for each step along the trackway, holding limb length ( $l_{fit}$ ) constant.

6. For each step, estimate the energy expenditure by body mass  $m$  and  $l_{fit}$ . Sum the estimations over all steps in order to produce the total energy expenditure ("Tot. en"). This parameter returns the total energy expenditure required to cover the entire trackway. Overall, we ran 100,000 randomizations repeating steps 1 to 6.

7. The total potential expenditure thus computed does not account for the scaling of the cost of locomotion, which is allometric in nature (CALDER, 1984). Indeed, it was demonstrated that body mass significantly affects energy expenditure during human walking (KRAMER, 2010). Large-bodied individuals have lower mass specific costs of locomotion. This means that the initial body size  $m$  will affect the cost of locomotion, so that minimum total expenditure will coincide with the largest possible body size. To remove this effect, after the randomizations were completed we regressed the body size  $m$  values to the corresponding total energy expenditure estimates and took the residuals. The lowest absolute residual this way corresponds to the single combination of  $m$ , fitted  $K$  values (along the entire trackway), and  $l_{fit}$  minimizing the total energy expenditure.

In order to verify that the shape of body mass distribution does not affect the results, we repeat the entire procedure by using a uniform distribution of body masses with the same range (40 to 90 kg) as the original distribution.

Once the best fit estimates for body size and limb lengths were found, we used them to feed allometric equations describing the relationships between limb length to stature in *Homo*. We used the equations in TROTTER & GLEESER (1952) and WILSON *et alii* (2010), which provide different equations for different ethnic groups. These equations allow to estimate stature starting from limb length measurement (femur + tibia) in *Homo*, and separately for the both sexes.

## RESULTS

We report individual step lengths ( $\lambda$ ) and slopes derived from the DOM for each footstep (Tab. 1, 2). The mean values of slope and  $\lambda$  along the trackway are  $-21.08^\circ$  and 0.542 m, respectively.

TABLE. 1

### Average slope measurements in degrees for each footstep.

Trackway A1 (11-14)		Trackway A2 (21-25)	
footstep	slope	footstep	slope
11-12	35.11	21-22	13.25
12-13	18.42	22-23	21.34
13-14	10.51	23-24	16.7
		24-25	28.87

TABLE. 2

### Step length measurements in meters for each step.

Trackway A1 (11-14)		Trackway A2 (21-25)	
Step	stepL ( $\lambda$ )	footstep	stepL ( $\lambda$ )
11-12	0.551	21-22	0.523
12-13	0.442	22-23	0.614
13-14	0.439	23-24	0.609
		24-25	0.619

The actual inter-footstep slope ranges from  $-35.11^\circ$  to  $-10.51^\circ$ . The highest value is observed over the first to second footprints, whereas the lowest values are observed at the mid-section of trackway.

As expected, the step length ( $\lambda$ ) changes as a function of slope. Yet, the regression between  $K_{fit}$  and either the slope or  $i$  values, are not significant (slope: p-value = 0.232,  $R^2 = 0.269$ ;  $i$  value: p-value=0.250,  $R^2=0.252$ , Tab. S2).

The average, best-fit potential energy expenditure per unit length, calculated for the normal body size distribution, equals to  $56,42 J * m^{-1}$  (corresponding to average value of 30.6 J per step, Tab. 3). The corresponding fitted  $K$  values have a mean of 1.436. The limb length estimate is 0.764 meters, and the body mass is 68.430 kg. The values of  $K$  along the trackway range from 1.23 to 1.74 (Tab. 3).

By using the uniform distribution, the best-fit body mass estimate is 66.235 kg (Tab. 4). This value is slightly lower than the body size estimated by using normal distribution. Consequently, the other related estimates follow the same trend. Limb length estimate is 0.734 m, whereas the potential energy expenditure, for 1 kg of mass transported along 1 meter, has an average value of  $0.833 J * kg^{-1} * m^{-1}$  (Tab. 4). It should be noted that although minor, the cost of kinetic energy contributes to total expenditure. This means our energetic estimate are conservative, and probably some 10% smaller than the actual figures.

By using the limb length estimate reported in the Tab. 3, we calculate the stature for Roccamonfina individual to be between 1.54 m and 1.63 m (Tab. 5). Very similar results are obtained by using the limb length estimated by applying the uniform distribution (see Tab. S1).

TABLE. 3

**The best-fit total potential energy expenditure for the normal body size distribution.**

$K$  values fitted by using likelihood function, limb length and body size estimated, energy expenditure per unit length over the entire trackway (Tot.en). Results were computed starting from normal body size distribution. Lw.B and Up.B are 95% confidence interval for body size estimate.

step	Fitted Ks	Lw.L	Limb Length (l)	Up.L	en.by.step (J*kg <sup>-1</sup> *step <sup>-1</sup> )	Slope (i)	Lw.B	Body size (kg)	Up.B	Tot.en (J * step <sup>-1</sup> )
11-12	1.387	0.758	0.764	0.771	0.668	0.703	67.980	68.430	68.863	45.738
12-13	1.729	0.758	0.764	0.771	0.390	0.333	67.980	68.430	68.863	26.672
13-14	1.741	0.758	0.764	0.771	0.256	0.185	67.980	68.430	68.863	17.497
21-22	1.462	0.758	0.764	0.771	0.317	0.235	67.980	68.430	68.863	21.717
22-23	1.245	0.758	0.764	0.771	0.469	0.391	67.980	68.430	68.863	32.074
23-24	1.255	0.758	0.764	0.771	0.391	0.300	67.980	68.430	68.863	26.773
24-25	1.235	0.758	0.764	0.771	0.640	0.631	67.980	68.430	68.863	43.772

TABLE. 4

**The best-fit total potential energy expenditure for the uniform body size distribution.**

$K$  values fitted by using likelihood function, limb length and body size estimated, energy expenditure for unit length over the entire trackway A (Tot.en). Results were computed starting from uniform body size distribution. Lw.L and Up.L are 95% confidence interval for limb length estimate. Lw.B and Up.B are 95% confidence interval for body size estimate.

step	Fitted Ks	Lw.L	Limb Length (l)	Up.L	en.by.step (J*kg <sup>-1</sup> *step <sup>-1</sup> )	Slope (i)	Lw.B	Body size (kg)	Up.B	Tot.en (J * step <sup>-1</sup> )
11-12	1.332	0.721	0.734	0.749	0.673	0.703	65.335	66.235	67.304	44.55
12-13	1.66	0.721	0.734	0.749	0.393	0.333	65.335	66.235	67.304	26.031
13-14	1.671	0.721	0.734	0.749	0.259	0.185	65.335	66.235	67.304	17.148
21-22	1.403	0.721	0.734	0.749	0.321	0.235	65.335	66.235	67.304	21.282
22-23	1.195	0.721	0.734	0.749	0.474	0.391	65.335	66.235	67.304	31.365
23-24	1.205	0.721	0.734	0.749	0.396	0.3	65.335	66.235	67.304	26.23
24-25	1.185	0.721	0.734	0.749	0.645	0.631	65.335	66.235	67.304	42.69

**DISCUSSION**

From the digital outcrop model it is evident that the trackway A has much shallower slope than the hillside itself. This suggests the Roccamonfina individual intentionally avoided the steepest slope, and despite moving upon a substrate of possibly warm ash, was comfortable enough not to run, as evidenced by the footprints spacing. This suggests that the assumption that the hominin moved using a comfortable path, which is also suggested by our approach (i.e. to minimize energy expenditure according its physiological constraints such as limb and step lengths), is probably correct.

The mean  $K$  of the path is 1.436. The  $K$  value shows little variation along the trackway, despite the great change in slope. The regression between  $K$  parameters against either slope and  $i$  values are in fact not significant, even if both regressions give a positive slope (Fig. S2). This result

confirms that the Roccamonfina hominin had not to adapt its step length to the optimal gradient. It should be noted that not any  $K$  is feasible due to physiological constraints. At  $K < 0.8$  the step length would become too large, and energy consumption would increase disproportionately, to be a sensible choice (SABORIT & CASINOS, 2015). On the other hand, large  $K$  values correspond to exceedingly short steps that, despite they do not require much energy, would lead to a small walking velocity, and again, be uncomfortable.

The Roccamonfina hominin was estimated to be some 68 kg, 1.60 m tall individual. This is bulkier than most modern humans, suggesting the individual might have been stocky built. This is common to Middle Pleistocene humans, as this small stature and heavy built has been shown to occur in both *H. heidelbergensis* and *H. neanderthalensis* (HELMUTH, 1998; RUFF, 2002).

Possibly the best body mass estimates in fossil *Homo* have been obtained by postcranial fossil remains (RUFF *et*



TABLE. 5

**Stature estimates.**

Different estimates following TROTTER & GLESER (1952), WILSON (2010) FSTAT, and WILSON (2010) ASTAT multiple regression equations. Lw and up represent the stature estimates starting from 95% confidence interval of limb length estimate.

<b>TROTTER &amp; GLESER (1952)</b>			
<b>Categories</b>	<b>lw</b>	<b>Stature</b>	<b>up</b>
Female EG1	158.575	159.453	160.301
Male EG1	161.842	162.664	163.456
Female EG2	155.24	156.036	156.804
Male EG2	158.221	158.947	159.649
<b>mean</b>	<b>158.469</b>	<b>159.275</b>	<b>160.052</b>

<b>WILSON (2010) FSTAT</b>			
<b>Categories</b>	<b>lw</b>	<b>Stature</b>	<b>up</b>
Female EG1	159.035	159.88	160.694
Male EG1	159.455	160.468	161.446
Female EG2	153.255	154.251	155.212
Male EG2	157.641	158.477	159.283
<b>mean</b>	<b>157.346</b>	<b>158.269</b>	<b>159.159</b>

<b>WILSON (2010) ASTAT</b>			
<b>Categories</b>	<b>lw</b>	<b>Stature</b>	<b>up</b>
Female EG1	159.194	160.035	160.846
Male EG1	160.105	161.072	162.004
Female EG2	156.336	157.183	158
Male EG2	158.35	159.168	159.958
<b>mean</b>	<b>158.496</b>	<b>159.365</b>	<b>160.202</b>

alii, 1997), and some cranial variables such as orbital area (KAPPELMAN, 1996; RIGHTMIRE, 2004) or orbital height (AIELLO & WOOD, 1994). However, the reliability of these estimates depends on sample size, which is an issue with the scarce Middle Pleistocene human fossil record. Furthermore, a number of estimates derives from regressions between pooled *Homo* samples (i.e. without separating among species). Body size within the hominin lineage tends to increase over time in keeping with Cope's rule (GRABOWSKI *et alii*, 2015; RAIA *et alii*, 2012; WILL *et alii*, 2018). Although there are exceptions to the pattern (i.e. *Homo naledi*, GARVIN *et alii*, 2017; *Homo floresiensis*, DINIZ-FILHO & RAIA, 2017) and large sized individuals appear even within australopiths (MASAO *et alii*, 2016) a marked increase seems nonetheless to have taken place, on average, with the appearance of *H. erectus s.l.* (ANTON *et alii*, 2014, GRABOWSKI *et alii*, 2015). RUFF (2002) found an increment in body mass of some 10% during the Middle Pleistocene with a peak at 500 ka. In agreement to Bergmann's rule (BERGMANN, 1848), this trend

is probably influenced by the inclusion of high-latitude *Homo* remains (RUFF *et alii*, 1997), but the magnitude of the shift suggests additional and non-exclusive causes, such as shift to high quality diet (AIELLO & WHEELER, 1995) or new behavioral responses to changing environments (GABUNIA *et alii*, 2000). Our results point to a 68.4 kg individual. This is very close to the average body mass (67.9 kg) reported for Middle Pleistocene *Homo* (RUFF *et alii*, 1997). This mass estimate is further close to the mean for 430 kyr Sima de los Huesos (Atapuerca) hominins at 69.1 kg (ARSUAGA *et alii*, 2014; 2015). These results indicate that the Roccamonfina individual perfectly fits the ecogeographical and temporal patterning in body mass evolution found for Middle Pleistocene *Homo* (HOLLIDAY, 1997; WILL *et alii*, 2018).

As regards the stature, as said above, we fitted a value of some 1.60 m, which still fits perfectly the Middle Pleistocene human body characteristics. CARRETERO *et alii* (2012) starting from both upper and lower limb remains of Sima de los Huesos individuals, reported a mean stature (male mean + female mean/2) of 163.6 cm, whereas the range of variation around this estimate spans from 1.56 cm to 1.68 cm when sexual dimorphism is considered (CARRETERO *et alii*, 2012). Perhaps unsurprisingly, the Roccamonfina individual estimated stature also coincides almost perfectly with *H. neanderthalensis* estimates (CARRETERO *et alii*, 2012; WILL *et alii*, 2018).

The features we predicted for the Roccamonfina hominin leave open the debate about attribution of these tracks to a given *Homo* species. Further studies more directly addressing the mark left on the surface by the walking individual (e.g. based on Winkler's individual index to derive body mass from footprint-induced substrate deformation). The temporal context does not allow to settle the issue, although the studied hominin seems to have been a normal sized individual, which moved comfortably well across the ashes of Roccamonfina volcano.

**CONCLUSION**

We aimed to explain how the Roccamonfina individual walked downhill along the slope gradient of Roccamonfina volcano. In addition, we derived some of its bodily features, as body size, limb length, and stature, from an explicit biomechanical model of human locomotion. The choice of such model is justified by the particular, oblique path the hominin took at walking through the trackways, which is expected by the model. The average *K* we fitted are very close to estimates for humans, including *H. sapiens*. Body mass and stature estimates for the Roccamonfina individual are consistent with Middle Pleistocene *Homo* remains.

**ACKNOWLEDGEMENTS**

The Spanish partners benefitted of funds from the project CGL2016-78577-P (Ministerio de Economía, Industria y Competitividad; Gobierno de España). We are grateful to Paul Palmqvist (Málaga, Spain) and two anonymous reviewers for suggestions and comments on early versions of this manuscript.

**REFERENCES**

AIELLO L.C. & WOOD B.A. (1994) - Cranial variables as predictors of hominine body mass. *Am. J. Phys. Anthropol.*, **95**, 409-426. <https://doi.org/10.1002/ajpa.1330950405>.

- AIELLO L.C. & WHEELER P. (1995) - *The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution*. *Cult. Anthropol.*, **36**, 199-221.
- ALEXANDER R.M.C.N. (1980) - *Optimum walking techniques for quadrupeds and bipeds*. *J. Zool.*, **192**, 97-117.
- ALEXANDER R.M.C.N. (1984) - *Stride length and speed for adults, children, and fossil hominids*. *Am. J. Phys. Anthropol.*, **63**, 23-27. <https://doi.org/10.1002/ajpa.1330630105>.
- ALEXANDER R.M.C.N. (1992) - *A model of bipedal locomotion on compliant legs*. *Phil. Trans. R. Soc. Lond. B.*, **338**, 189-198.
- ANTÓN S.C., POTTS R. & AIELLO L.C. (2014) - *Evolution of early Homo: an integrated biological perspective*. *Science*, **345**, 45-58. <https://doi.org/10.1126/science.1236828>.
- ARSUAGA J.L., CARRETERO J.M., LORENZO C., GÓMEZ-OLIVENCIA A., PABLOS A., RODRÍGUEZ L., GARCÍA-GONZÁLEZ R., BONMATÍ A., QUAM R.M., PANTOJA-PÉREZ A., MARTÍNEZ I., ARANBURU A., GRACIA-TÉLLEZ A., POZA-REY E., SALA N., GARCÍA N., ALCÁZAR DE VELASCO A., CUENCA-BESCÓS G., MARÍA BERMÚDEZ DE CASTRO J. & CARBONELL E. (2015) - *Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain*. *Proc. Natl. Acad. Sci.*, **112**, 11524-11529. <https://doi.org/10.1073/pnas.1514828112>.
- ARSUAGA J.L., MARTÍNEZ I., ARNOLD L.J., ARANBURU A., GRACIA-TÉLLEZ A., SHARP W.D., QUAM R.M., FALGUÉRES C., PANTOJA-PÉREZ A., BISCHOFF J., POZA-REY E., PARÉS J.M., CARRETERO J.M., DEMURO M., LORENZO C., SALA N., MARTÍN-TORRES M., GARCÍA N., ALCÁZAR DE VELASCO A., CUENCA-BESCÓS G., GÓMEZ-OLIVENCIA A., MORENO D., PABLOS A., SHEN C.C., RODRÍGUEZ L., ORTEGA A.I., GARCÍA R., BONMATÍ A., BERMÚDEZ DE CASTRO J.M. & CARBONELL E. (2014) - *Neanderthal roots: Cranial and chronological evidence from Sima de los Huesos*. *Science*, **344**, 1358-1363 <https://doi.org/10.1126/science.1253958>.
- ASHTON N., LEWIS S.G., DE GROOTE I., DUFFY S.M., BATES M., BATES R., PETER H., LEWIS M., SIMON A.P., SYLVIA P., WILLIAMS C. & STRINGER C. (2014) - *Hominin footprints from early Pleistocene deposits at Happisburgh, UK*. *PLoS One*, **9**, e88329. <https://doi.org/10.1371/journal.pone.0088329>.
- AVANZINI M., MIETTO P., PANARELLO A., DE ANGELIS M. & ROLANDI G. (2008) - *The devil's trails: Middle pleistocene human footprints preserved in a volcanoclastic deposit of southern Italy*. *Ichnos*, **15**, 179-189. <https://doi.org/10.1080/10420940802470458>.
- BENNETT M.R. & MORSE S.A. (2014) - *Human footprints: fossilised locomotion?* Springer, New York.
- BERGMANN C. (1848) - *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. *Göttinger studies*, **3**, pt. 1, 595-708.
- CALDER W.A. (1984) - *Size, function, and life history*. Harvard University Press, Cambridge.
- CARRETERO J.M., RODRÍGUEZ L., GARCÍA-GONZÁLEZ R., ARSUAGA J. L., GÓMEZ-OLIVENCIA A., LORENZO C., BONMATÍ A., GRACIA A., MARTÍNEZ I. & QUAM R. (2012) - *Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain)*. *J. Hum. Evol.*, **62**, 242-255. <https://doi.org/10.1016/j.jhevol.2011.11.004>.
- CAVAGNA G.A. & KANEKO M. (1977) - *Mechanical work and efficiency in level walking and running*. *J. Physiol.*, **268**, 467-481.
- DINIZ-FILHO J.A.F. & RAIA P. (2017) - *Island Rule, quantitative genetics and brain-body size evolution in Homo floresiensis*. *Proc. R. Soc. B*, **284**, 20171065. <https://doi.org/10.1098/rspb.2017.1065>.
- ENDICOTT P., HO S.Y. & STRINGER C. (2010) - *Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins*. *J. Hum. Evol.*, **59**, 87-95. <https://doi.org/10.1016/j.jhevol.2010.04.005>.
- FAVALLI M., FORNACIAI A., ISOLA I., TARQUINI S. & NANNIPIERI L. (2012) - *Multiview 3D reconstruction in geosciences*. *Computat. Geosci.*, **44**, 168-176. <https://doi.org/10.1016/j.cageo.2011.09.012>.
- GABUNIA L., VEKUA A., LORDKIPANIDZE D., SWISHER C.C., FERRING R., JUSTUS A., NIORADZE M., TVALCHRELDZE M., ANTÓN C.S., BOSINSKI G., JÖRIS O., DE LUMLEY M. A., MAJSURADZE G. & MOUSKHELISHVILI A. (2000) - *Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age*. *Science*, **288**, 1019-1025. <https://doi.org/10.1126/science.288.5468.1019>.
- GARVIN H.M., ELLIOTT M.C., DELEZENE L.K., HAWKS J., CHURCHILL S.E. & BERGER L.R. HOLLIDAY T.W. (2017) - *Body size, brain size, and sexual dimorphism in Homo naledi from the Dinaledi Chamber*. *J. Hum. Evol.*, **111**, 119-138. <https://doi.org/10.1016/j.jhevol.2017.06.010>.
- GIERLIŃSKI G.D., NIEDZWIEDZKI G., LOCKLEY M.G., ATHANASSIOU A., FASSOULAS C., DUBICKA Z., BOCHAROWSKI A., BENNETT M.R. & AHLBERG P.E. (2017) - *Possible hominin footprints from the late Miocene (c. 5.7 Ma) of Crete?*. *P. Geologist. Assoc.*, **128**, 697-710. <https://doi.org/10.1016/j.pgeola.2017.07.006>.
- GRABOWSKI M., HATALA K.G., JUNGERS W.L. & RICHMOND B.G. (2015) - *Body mass estimates of hominin fossils and the evolution of human body size*. *J. Hum. Evol.*, **85**, 75-93. <https://doi.org/10.1016/j.jhevol.2015.05.005>.
- GRUSS L.T. (2007) - *Limb length and locomotor biomechanics in the genus Homo: an experimental study*. *Am. J. Phys. Anthropol.*, **134**, 106-116.
- HATALA K.G., ROACH N.T., OSTROFSKY K.R., WUNDERLICH R.E., DINGWALL H.L., VILLMOARE B.A., GREEN D.J., HARRIS J.W.K., BRAUN D.R. & RICHMOND B.G. (2016) - *Footprints reveal direct evidence of group behavior and locomotion in Homo erectus*. *Sci. Rep.*, **6**, 28766. <https://doi.org/10.1038/srep28766>.
- HELMUTH H. (1998) - *Body height, body mass and surface area of the Neanderthals*. *Z. Morphol. Anthropologie*, 1-12.
- HOLLIDAY T.W. (1997) - *Postcranial evidence of cold adaptation in European Neanderthals*. *Am. J. Phys. Anthropol.*, **104**, 245-258. [https://doi.org/10.1002/\(SICI\)1096-8644\(199710\)104:2%3C245::AID-AJPA10%3E3.0.CO;2-%23](https://doi.org/10.1002/(SICI)1096-8644(199710)104:2%3C245::AID-AJPA10%3E3.0.CO;2-%23).
- KAPPELMAN J. (1996) - *The evolution of body mass and relative brain size in fossil hominids*. *J. Hum. Evol.*, **30**, 243-276. <https://doi.org/10.1006/jhev.1996.0021>.
- KRAMER P.A. & ECK G.G. (2000) - *Locomotor energetics and leg length in hominid bipedality*. *J. Hum. Evol.*, **38**, 651-666. <https://doi.org/10.1006/jhev.1999.0375>.
- KRAMER P.A. (2010) - *The effect on energy expenditure of walking on gradients or carrying burdens*. *Am. J. Hum. Biol.*, **22**, 497-507. <https://doi.org/10.1002/ajhb.21027>.
- LOCKLEY M., KIM J.Y. & ROBERTS G. (2007) - *The ichnos project: a re-evaluation of the hominid track record*. In: Lucas S.G., Spielmann J.A., Lockley M.G. (Eds.), *Cenozoic Vertebrate Tracks and Traces*. New Mexico Museum of Natural History & Science, Albuquerque, Bulletin, **42**, 42-79.
- LOCKLEY M., ROBERTS G. & KIM J.Y. (2008) - *In the footprints of our ancestors: an overview of the hominid track record*. *Ichnos*, **15**, 106-125. <https://doi.org/10.1080/10420940802467835>.
- MARGARIA R. (1976) - *Biomechanics and energetics of Muscular Exercise*. Oxford University Press, USA.
- MASAO F.T., ICHUMBAKI E.B., CHERIN M., BARILI A., BOSCHIAN G., IURINO D.A., MENCONERO S., MOGGI-CECCHI J. & MANZI G. (2016) - *New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins*. *Elife*, **5**, e19568. <https://doi.org/10.7554/eLife.19568>.
- MIETTO P., AVANZINI M. & ROLANDI G. (2003) - *Palaeontology: Human footprints in Pleistocene volcanic ash*. *Nature*, **422**, 133-133.
- MINETTI A.E., MOIA C., ROI G.S., SUSTA D. & FERRETTI G. (2002) - *Energy cost of walking and running at extreme uphill and downhill slopes*. *J. Appl. Physiol.*, **93**, 1039-1046.
- PANARELLO A., SANTELLO L., FARINARO G., BENNETT M.R. & MIETTO P. (2017) - *Walking along the oldest human fossil pathway (Roccamonfina volcano, Central Italy)?*. *J. Archaeol. Sci.: Reports*, **13**, 476-490. <https://doi.org/10.1016/j.jasrep.2017.04.020>.
- PANARELLO A. (2016) - *Elementi di Paleoicnologia degli Ominidi*. Armando Caramanica Editore, Marina di Minturno.
- RAIA P., CAROTENUTO F., PASSARO F., FULGIONE D. & FORTELIUS M. (2012) - *Ecological specialization in fossil mammals explains Cope's rule*. *Am. Nat.*, **179**, 328-337. <https://doi.org/10.5061/dryad.8bn8431n>.
- RAICHLER D.A., PONTZER H. & SOCKOL M.D. (2008) - *The Laetoli footprints and early hominin locomotor kinematics*. *J. Hum. Evol.*, **54**, 112-117. <https://doi.org/10.1016/j.jhevol.2007.07.005>.
- REMONDINO F. & EL-HAKIM S. (2006) - *Image-based 3D modelling: A review*. *Photogrammetric Rec.*, **21**, 269-291.
- RIGHTMIRE G.P. (2004) - *Brain size and encephalization in Early to Mid-Pleistocene Homo*. *Am. J. Phys. Anthropol.*, **124**, 109-123. <https://doi.org/10.1002/ajpa.10346>.
- RUE M.J. & KRAMER P.A. (2017) - *Minimal energetic expenditure of women walking burdened on gradients in urban environments*. *Am. J. Hum. Biol.*, **29**, <https://doi.org/10.1002/ajhb.22907>.
- RUFF C. (2002) - *Variation in human body size and shape*. *Annu. Rev. Anthropol.*, **31**, 211-232. <https://doi.org/10.1146/annurev.anthro.31.040402.085407>.



- RUFF C.B., TRINKAUS E. & HOLLIDAY T.W. (1997) - *Body mass and encephalization in Pleistocene Homo*. *Nature*, **387**, 173.
- SABORIT G. & CASINOS A. (2015) - *Parametric modeling of human gradient walking for predicting minimum energy expenditure*. *Comput. Math. Method. M.* <https://doi.org/10.1155/2015/407156>.
- SANTELLI L. (2010) - *Analysis of a trampled formation: the Brown Leucitic Tuff (Roccamonfina volcano, Southern Italy)*. Ph.D. Thesis in "Scienze della Terra", Università degli Studi di Padova, Dipartimento di Geoscienze.
- SCAILLET S., VITA-SCAILLET G. & GUILLOU H. (2008) - *Oldest human footprints dated by Ar/Ar*. *Earth Planet. Sc. Lett.*, **275**, 320-325. <https://doi.org/10.1016/j.epsl.2008.08.026>.
- SCHAEFFER P.J. & LINDSTEDT S.L. (2013) - *How animals move: comparative lessons on animal locomotion*. *Compr. Physiol.*, **3**, 289-314.
- SELLERS W.I., CAIN G.M., WANG W. & CROMPTON R.H. (2005) - *Stride lengths, speed and energy costs in walking of Australopithecus afarensis: using evolutionary robotics to predict locomotion of early human ancestors*. *J. Royal Soc. Interface*, **2**, 431-441. <https://doi.org/10.1098/rsif.2005.0060>.
- STEUDEL-NUMBERS K.L., WEAVER T.D. & WALL-SCHEFFLER C.M. (2007) - *The evolution of human running: effects of changes in lower-limb length on locomotor economy*. *J. Hum. Evol.*, **53**, 191-196. <https://doi.org/10.1016/j.jhevol.2007.04.001>.
- TAVANI S., CORRARETTI A. & BILLI A. (2016) - *High precision analysis of an embryonic extensional fault-related fold using 3D orthorectified virtual outcrops: The viewpoint importance in structural geology*. *J. Struct. Geol.*, **86**, 200-210. <https://doi.org/10.1016/j.jsg.2016.03.009>.
- TROTTER M. & GLESER G.C. (1952) - *Estimation of stature from long bones of American Whites and Negroes*. *Am. J. Phys. Anthropol.*, **10**, 463-514.
- VIDAL-CORDASCO M., MATEOS A., ZORRILLA-REVILLA G., PRADO-NÓVOA O. & RODRÍGUEZ J. (2017) - *Energetic cost of walking in fossil hominins*. *Am. J. Phys. Anthropol.*, **164**, 609-622. <https://doi.org/10.1002/ajpa.23301>.
- WHITE T.D. & SUWA G. (1987) - *Hominid footprints at Laetoli: facts and interpretations*. *Am. J. Phys. Anthropol.*, **72**, 485-514. <https://doi.org/10.1002/ajpa.1330720409>.
- WILL M., PABLOS A. & STOCK J.T. (2017) - *Long-term patterns of body mass and stature evolution within the hominin lineage*. *Royal Soc. Open Sci.*, **4**, 171339. <https://doi.org/10.1098/rsos.171339>.
- WILKINSON M.J. & MENZ H.B. (1997) - *Measurement of gait parameters from footprints: a reliability study*. *The foot*, **7**, 19-23.
- WILSON R.J., HERRMANN N.P. & JANTZ L.M. (2010) - *Evaluation of stature estimation from the database for forensic anthropology*. *J. Forensic Sci.*, **55**, 684-689. <https://doi.org/10.1111/j.1556-4029.2010.01343.x>.

Manuscript received 23 November 2018; accepted 26 January 2019; published online 30 January 2019;  
editorial responsibility and handling by Lorenzo Rook