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**From footprint morphometrics to the stature of fossil hominins:
A common but uncertain estimate**

**De la morphométrie des empreintes de pieds à la stature des hominines
fossiles : une estimation fréquente mais incertaine**

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Abstract

Hominin footprints are a particular remain in paleoanthropology representing brief moments of life of extinct individuals. Footprints not only provide information on the locomotor behavior of fossil taxa but also on their body characteristics such as their stature. This stature is usually estimated from the length of the footprints based on the well-known foot length to stature ratio. However, footprint length does not result only from the foot length but of a combination of factors. Therefore, it is necessary to investigate the relationships between footprint length and stature of individuals using experimental approaches. Secondly, recent discoveries of fossil footprints have led to the estimation of statures from isolated footprints. However, such estimates may be biased because of the intraindividual morphometric variation of the footprints. Moreover, footprints may also be incomplete making it impossible to measure the length and therefore the estimation of a stature. The search for relationships between stature and other morphometric variables is therefore necessary to have the most accurate picture possible of the individuals who left these tracks. In this context, this article reports the results of an experimental study that aims to determine the relationships between the stature of individuals and different morphometric variables and to quantify the intraindividual variation of each variable. Thus, 21 morphometric variables were measured on a total of 175 experimental footprints left by 20 individuals in an experimental area composed of loose sand. Statistical analyses show that footprint lengths are not only the variables most correlated with stature but also those with the least intraindividual variation. However, estimation of stature from footprints left by fossil hominins is subject to three types of uncertainties: residuals from linear regression, intraindividual variation that can be particularly large in soft substrates, and the application of relationships defined on modern populations to fossil taxa.

Résumé

Les empreintes de pieds d'hominines sont des vestiges particuliers en paléanthropologie offrant un point de vue sur de brefs moments de vie d'individus disparus. Les empreintes apportent non seulement des informations sur le comportement locomoteur des taxons fossiles mais également sur leurs caractéristiques corporelles telles que leur stature. Cette stature est généralement estimée à partir de la longueur des empreintes sur la base du rapport bien connu entre la longueur du pied et la stature. Toutefois, la longueur de l'empreinte ne résulte pas uniquement de la longueur du pied mais d'une combinaison de facteurs. Par conséquent, il est nécessaire de rechercher les relations entre la longueur des empreintes et la stature des individus au moyen d'approches expérimentales. Par ailleurs, les récentes découvertes d'empreintes fossiles ont conduit à estimer des statures à partir d'empreintes isolées. Or, de telles estimations peuvent être biaisées à cause de la variation morphométrique intra-individuelle des empreintes. De plus, les empreintes peuvent être non seulement isolées mais également incomplètes. Il est parfois impossible de mesurer leur longueur et donc d'en estimer une stature. La recherche de relations entre la stature et d'autres variables morphométriques est donc nécessaire pour avoir l'image la plus précise possible des individus ayant laissé ces empreintes. Dans ce contexte, cet article rapporte les résultats d'une étude expérimentale ayant pour but de déterminer les relations entre la stature des individus et différentes variables morphométriques puis de quantifier la variation intra-individuelle de chaque variable. Ce sont ainsi 21 variables morphométriques qui ont été mesurées sur un total de 175 empreintes laissées par 20 individus au sein d'une aire expérimentale composée de sable meuble. Les analyses statistiques montrent que les longueurs des empreintes sont non seulement les variables les plus corrélées à la stature mais également celles ayant la variation intra-individuelle la plus faible. Toutefois, l'estimation de la stature à partir d'empreintes de pieds laissées par des hominines fossiles est soumise à trois types d'incertitudes : les résidus de la régression linéaire, la variation intra-individuelle pouvant être particulièrement importante dans des substrats meubles et l'application de relations définies sur des populations modernes à des taxons fossiles.

Keywords: Footprints, Morphometrics, Variation, Stature, Experimentation, Hominins,

Mots clés : Empreintes de pieds, Morphométrie, Variation, Stature, Expérimentation, Hominines

1. Introduction

Hominin footprints represent a particular remain in paleoanthropology. While they were scarce in the fossil record until the 2010s (Leakey and Hay, 1979, Bennett et al., 2009, Lockley et al., 2009), they have become in the last ten years a more and more common material thanks to discoveries in all regions and for periods ranging from the Upper Miocene to the Holocene (Ashton et al., 2014, Masao et al., 2016, Gierliński et al., 2017, Ledoux et al., 2017, Altamura et al., 2018, Bustos et al., 2018, Helm et al., 2018, Dubeau et al., 2019, Stewart et al., 2020, Bennett et al., 2021, Mayoral et al., 2021, McNutt et al., 2021, Zhang et al., 2021).

The main particularity of footprints comes from the temporal scale they represent: very brief moments of life comparable to snapshots (Mastrolorenzo et al., 2006, Falkingham, 2014, Hatala

et al., 2020, Stewart et al., 2020, Duveau, 2021). Indeed, footprints from a single surface are formed over a very short period since they must be quickly covered by sediment in order to be preserved, especially for outdoor sites where they are subject to numerous taphonomic agents such as wind, tide or precipitation (Marty et al., 2009, Bennett and Morse, 2014, Wiseman and De Groote, 2018). Hominin footprints, because of this window on moments of life, therefore differ from the more common skeletal remains that provide a more or less reliable representation of the individual at the time of his death and some life history data (Hemmer, 2007, Stodder, 2018).

Thanks to this particular temporal scale, footprints provide many original information. They inform on the locomotor behaviour (Bennett and Morse, 2014, Bennett et al., 2016, Hatala et al., 2016a, Hatala et al., 2016b, Hatala et al., 2016c, McNutt et al., 2021) but also the functional anatomy (Duveau et al., 2019, Wiseman et al., 2020) of the individuals who made them. The famous Laetoli trackways are the most telling example since they represent the first direct evidence of human bipedalism used by fossil hominins (Leakey and Hay, 1979, Masao et al., 2016, McNutt et al., 2021). However, the most common information estimated from the footprints are body characteristics such as body mass (Robbins, 1986, Dingwall et al., 2013, Bennett and Morse, 2014, Domjanic et al., 2015, Ruff et al., 2021) and especially and more commonly the stature of individuals (Ashton et al., 2014, Masao et al., 2016, Altamura et al., 2018, Bustos et al., 2018, Helm et al., 2018, Duveau et al., 2019, Bennett et al., 2021, Mayoral et al., 2021, Zhang et al., 2021). Such information gives access to the composition and the behaviours of the track-maker groups (Hatala et al., 2016c, Roach et al., 2016, Bustos et al., 2018, Duveau et al., 2019, Mayoral et al., 2021). Estimates of these body characteristics from footprints are not only useful in a paleoanthropological context but also in clinical studies or to estimate the body characteristics of suspects in criminal cases (Krishan, 2008, Kanchan et al., 2012, Reel et al., 2012, Hemy et al., 2013, Švábová et al., 2022).

The estimation of stature, and more generally of other body characteristics, from footprints can be done following two methodological approaches: either by observations and interpretations of expert trackers (Pastoors et al., 2015, Pastoors et al., 2017) or by the use of relationships linking these body characteristics to the morphometry of the footprints (Dingwall et al., 2013, Bennett and Morse, 2014, Wiseman and De Groote, 2022). In the morphometric approach, stature is usually estimated based on the foot length to stature ratio (14–15%) (Bégouën and Vallois, 1927, Pales and Saint-Péreuse, 1976, Citton et al., 2017) known since the anthropometric studies of the end of the 19th century (Topinard, 1877, Martin, 1928).

However, the morphology of a footprint, and therefore its dimensions, is not just the result of the morphology of the foot. It is notably impacted by the characteristics of the gait of the track-makers, such as speed (Dingwall et al., 2013, Wiseman and De Groote, 2022) or the distribution of plantar pressures (Crompton and Pataky, 2009, Crompton et al., 2012, Bates et al., 2013, Hatala et al., 2016a, Hatala et al., 2016b). The nature of the substrate, such as its granulometry, humidity or rigidity, has also a strong impact on the footprint morphology (Allen, 1997, Milàn and Bromley, 2007, D'Août et al., 2010, Bennett and Morse, 2014). Finally, this morphology is also impacted by taphonomic agents damaging or destroying certain parts of the prints (Marty et al., 2009, Bennett and Morse, 2014, Roach et al., 2016, Wiseman and De Groote, 2018). In this context, more and more studies emphasize the need to use an experimental framework in order to quantify the

relationship between footprint length and stature and not only between foot length and stature (Dingwall et al., 2013, Bennett and Morse, 2014, Wiseman and De Groote, 2022). The use of such experimental frameworks is done under controlled conditions close to those where fossil footprints were found, thus allowing for more precise paleobiological estimates for each site.

Some of these experimental studies have highlighted the intraindividual morphological variation of the footprints (Morse et al., 2013, Belvedere et al., 2021, Wiseman and De Groote, 2022) in particular in deformable loose sandy substrates in which several fossil footprints have recently been discovered (Morse et al., 2013, Altamura et al., 2018, Bustos et al., 2018, Duveau et al., 2019, Mayoral et al., 2021). This intraindividual variation must be taken into account when studying fossil footprints and more specifically when only isolated footprints, which cannot be associated within a trackway, are discovered. When such isolated footprints are found, the knowledge of intraindividual variation has been used to estimate minimum numbers of individuals (Webb et al., 2014, Duveau et al., 2019, Belvedere et al., 2021). But this knowledge is more rarely applied to stature estimates whereas because of the intraindividual dispersion, the estimation of stature on an isolated footprint is uncertain.

Finally, both studies on the relationship between footprint morphometry and body characteristics and those on intraindividual morphological variation are mainly based on footprint length (Dingwall et al., 2013, Morse et al., 2013, Belvedere et al., 2021, Wiseman and De Groote, 2022). This variable is not only easily measured but also strongly correlated with individual stature. However, there are many examples of incomplete footprints within the fossil record for which it is impossible to measure this length (Onac et al., 2005, Ashton et al., 2014, Duveau et al., 2019, Mayoral et al., 2021). It would therefore be necessary to study the correlation between individual stature and other morphometric variables than length in order to know if it is possible to estimate stature from incomplete footprints.

In this context, this article reports the results of an exploratory experimental study aimed at quantifying the relationships and their uncertainties between different morphometric variables of experimental footprints and the stature of individuals. It is divided into two independent parts. The first part seeks to quantify the relationships between each morphometric variable and the stature of individuals, thus giving reference points to ichnologists wishing to estimate statures from incomplete footprints. The second part aims at determining the intraindividual variation of each morphometric variable used in order to know the uncertainties when estimating stature on isolated prints. All of these results will then be discussed, focusing in particular on the application of the experimental relationships to footprints made by fossil hominin taxa.

2. Material and methods

2.1. Material

The material for this study consists of 175 experimental footprints made by 20 individuals who volunteered (Fig. 1). Each volunteer was informed of the objectives of the experiment and gave their signed consent, or that of their legal guardian in the case of minors. Beforehand, they were asked to provide their age and to confirm the absence of any pathology that could affect the

morphology of their foot or their gait. Their stature and the length of their feet (distance between the base of the heel and the end of the second toe) were then measured (Table 1). The 20 individuals ranged in age from 11 to 36 years (mean: 23 years), in stature from 146.0 to 182.3 cm (mean: 167 cm), and in foot length from 20.4 to 26.6 cm (mean 23.3 cm). There was no significant difference between right and left foot length (Student's t-test: $P \gg 0.05$). Age, stature, and foot length each followed a normal distribution (Shapiro–Wilk: $P \gg 0.05$; Fig. 2).

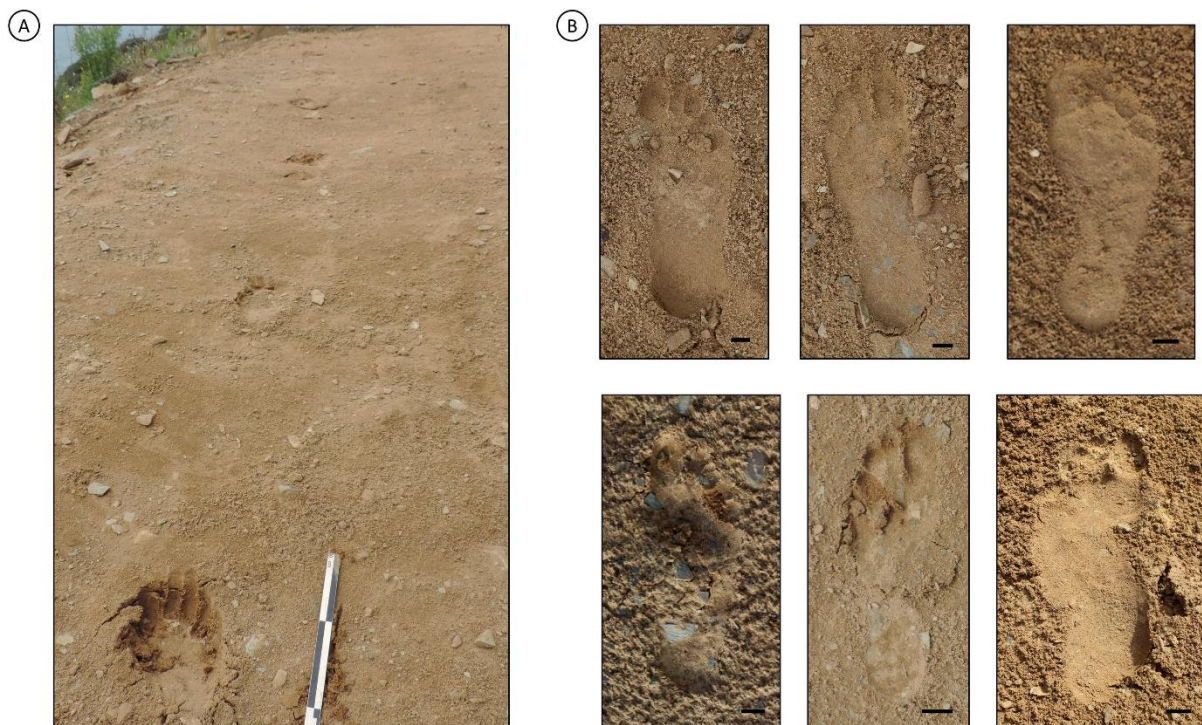


Fig. 1. Experimental trackway (A) and footprints (B) (black scale bar: 2 cm).

Piste (A) et empreintes de pieds expérimentales (B) (barre d'échelle noire : 2 cm).

Table 1. Features of the individuals who made the experimental footprints.

Caractéristiques des individus ayant réalisé les empreintes expérimentales.

Individual	Sex	Age (years)	Foot length (cm)	Stature (cm)	Foot length/stature	Number of footprints
I1	Female	13	22.4	153.9	14.6%	11
I2	Male	22	24.4	177.1	13.8%	8
I3	Female	22	21.8	166.9	13.1%	15
I4	Female	13	20.5	153.8	13.3%	8
I5	Male	31	23.7	171.2	13.8%	14
I6	Female	22	24.1	175.8	13.7%	16
I7	Female	34	23.1	160.0	14.4%	10
I8	Female	36	25.5	171.8	14.8%	6
I9	Male	23	23.3	182.3	12.8%	11
I10	Male	23	25.3	170.8	14.8%	11
I11	Female	28	26.6	172.9	15.4%	6
I12	Male	19	26.2	173.5	15.1%	9
I13	Female	11	21.5	146.0	14.7%	3
I14	Female	21	22.7	169.0	13.4%	7
I15	Male	21	25.0	178.5	14.0%	8
I16	Female	34	24.0	172.0	14.0%	6
I17	Female	24	20.7	157.0	13.2%	6
I18	Female	25	22.6	162.0	14.0%	4
I19	Female	21	20.4	156.0	13.0%	6
I20	Male	22	23.3	171.8	13.5%	10
Minimum		11.0	20.4	146.0	12.8%	3
Mean		23.3	23.3	167.1	14.0%	9
Maximum		36.0	26.6	182.3	15.4%	16

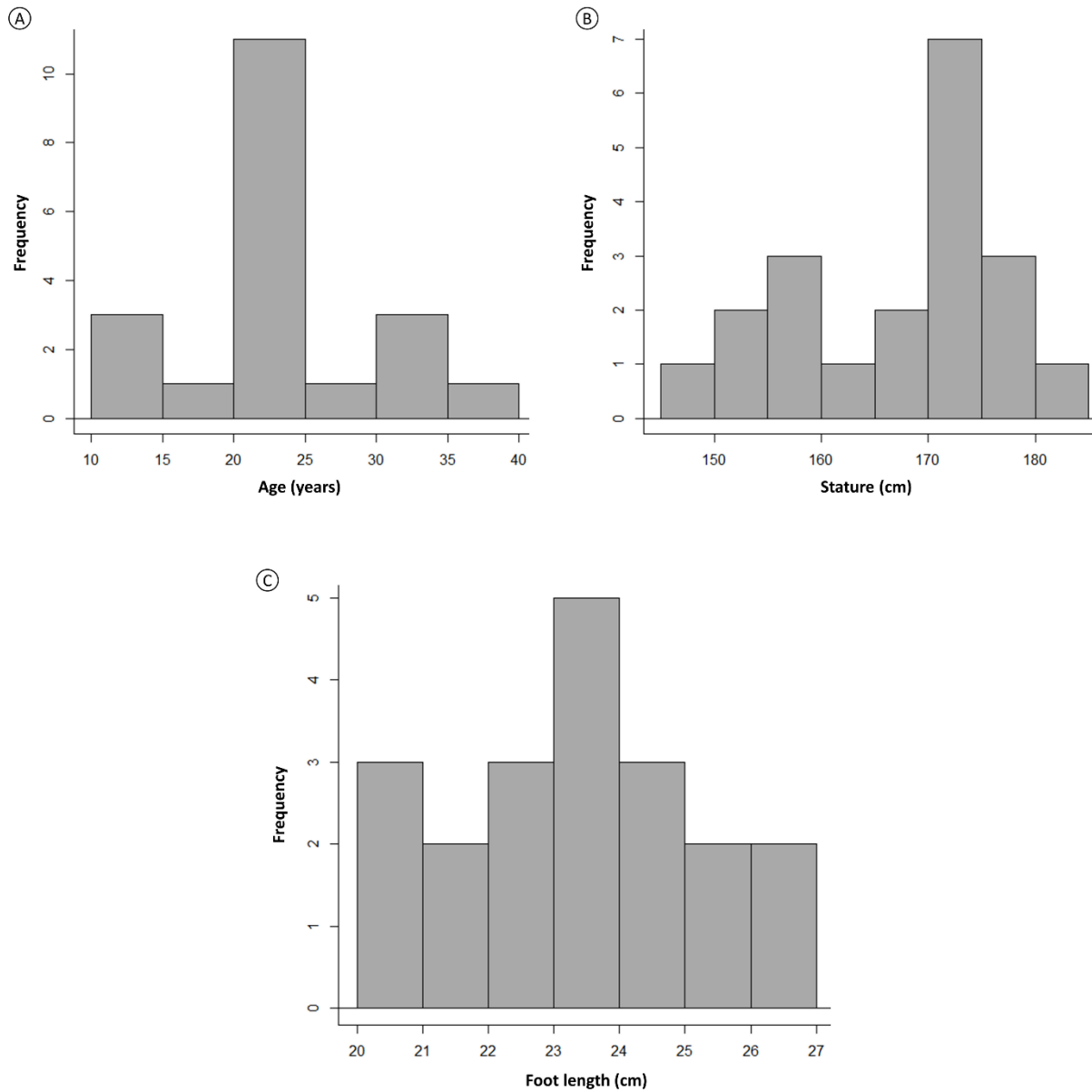


Fig. 2. Histograms of biological characteristics of participants who made the experimental footprints. A. Age distribution. B. Stature distribution. C. Foot length distribution.

Histogrammes des caractéristiques biologiques des participants ayant réalisé les empreintes de pieds expérimentales. A. Distribution des âges. B. Distribution des statures. C. Distribution des longueurs des pieds.

After measuring the biological features of the participants, they were asked to progress barefoot through an experimental area using a walk that they considered habitual and comfortable (Fig. 1). This experimental area has a flat topography and is composed of a wet sand with a fine to medium grain size (the majority of the grains having a size exceeding 250 μm). This type of particularly loose sandy substrate is similar to many sites where fossil hominin footprints have been discovered (Altamura et al., 2018, Bustos et al., 2018, Duveau et al., 2019, Mayoral et al., 2021).

At the end of each experimental sequence, each footprint made was described, measured in situ and photographed. Among the 175 footprints, 49 footprints were digitized in 3D by photogrammetry by using Agisoft Metashape (v.1.7.0) and a photographic coverage taken with a Canon EOS 1300D. In order to share the data within the scientific community, all these experimental footprints will be incorporated into a database where they can be freely downloaded. While waiting for this integration in this database, they can be obtained on request from the author.

2.2. Methods

2.2.1. Morphometric variables

The analyses of correlations between footprint morphometry and individual stature and the study of intraindividual morphometric variation are based on 21 morphometric variables, 16 linear measurements and 5 surface measurements (Fig. 3, Fig. 4, Appendix A). The objective was to consider as many variables as possible from the footprints and not only their length. Not all of these 21 variables could be measured on each of the 175 experimental footprints because of the impossibility of observing some landmarks either because the landmark was not sufficiently marked or because of sediment deposition in the area of the landmark following the foot movement.

The 16 linear measurements are divided into 12 length and 4 width measurements. The first five lengths are referred to as total lengths and correspond to the distance between the base of the heel and the tip of each of the 5 toes ($L_{\text{tot}1}$ to $L_{\text{tot}5}$, Fig. 3). The next five lengths are referred to as tarsometatarsal because they correspond to the length between the base of the heel and the middle of each rim separating the toes from the rest of the footprint ($L_{\text{tmt}1}$ to $L_{\text{tmt}5}$, Fig. 3). In the case of a loose and deformable sediment such as the one in the experimental area, sedimentary displacement toward the back of the footprint is often observed as a result of toe propulsion during walking. Therefore, these tarsometatarsal lengths are not always measurable. Finally, the last two lengths correspond to the distance between the base of the heel and the most medial (L_{med}) and lateral (L_{lat}) points of the front of the footprints (Fig. 3). These points correspond anatomically to the ends of the metatarsal heads: the medial end of the first metatarsal for the medial length and the lateral end of the fifth metatarsal for the lateral length.

Of the 4 widths, 3 were measured along the mediolateral axis of the footprint, which is perpendicular to the longitudinal axis passing through the base of the heel and the tip of the second toe. These are the maximum heel width (W_{prox}), the minimum midfoot width (W_{mid}), and

the maximum forefoot width (W_{dist}) (Fig. 3). The fourth width is the distance from the tip of the hallux to the tip of the fifth toe (W_{toes} , Fig. 3).

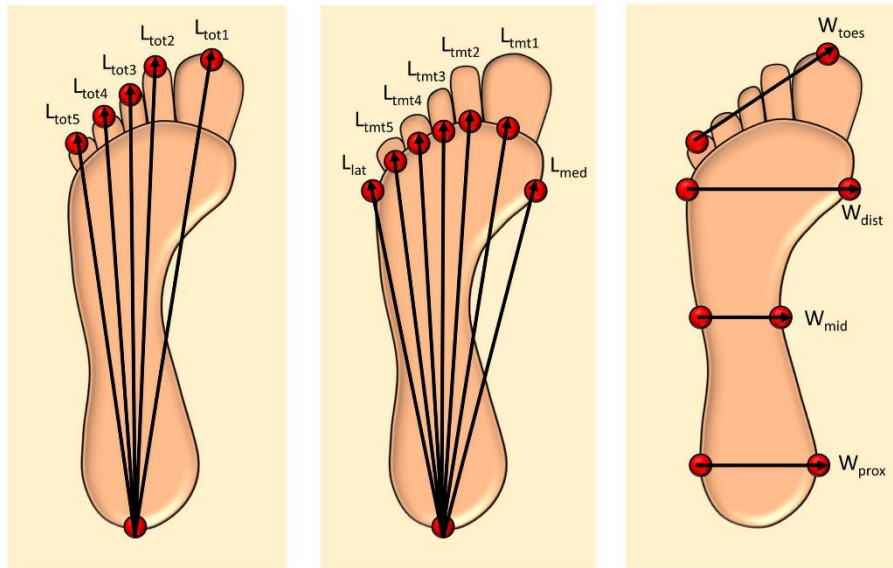
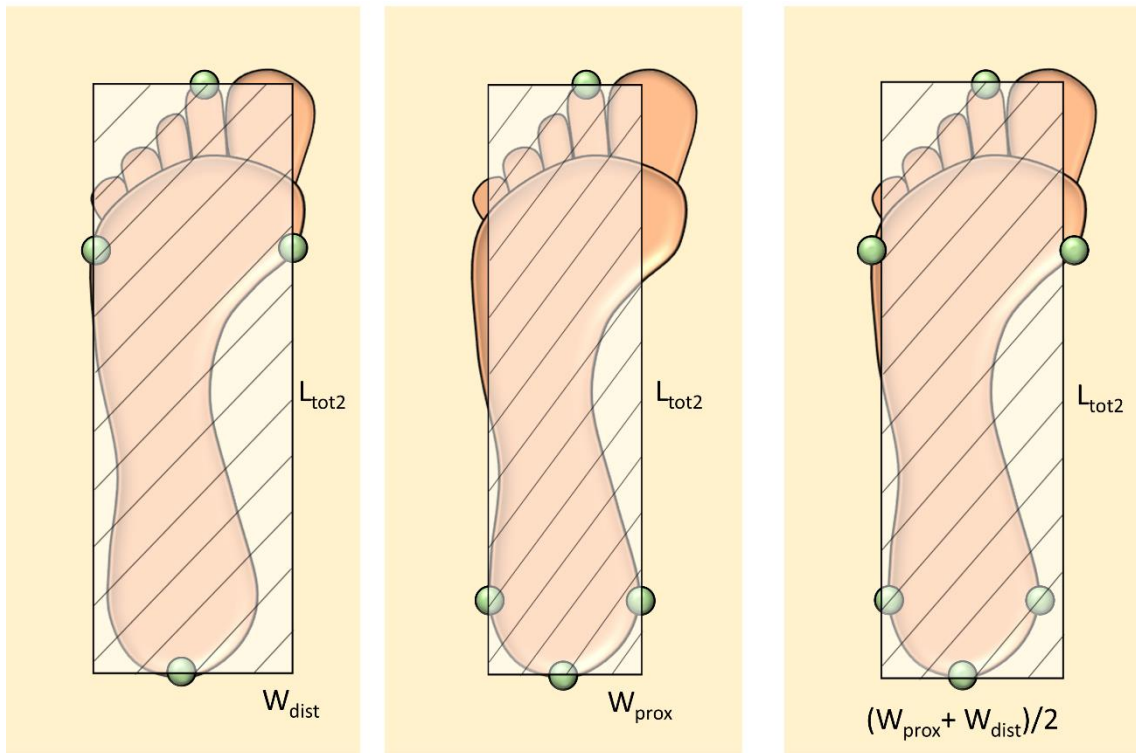


Fig. 3. Dimensions measured on the experimental footprints. L_{tot1} : total length 1; L_{tot2} : total length 2; L_{tot3} : total length 3; L_{tot4} : total length 4; L_{tot5} : total length 5; L_{tmt1} : tarsometatarsal length 1; L_{tmt2} : tarsometatarsal length 2; L_{tmt3} : tarsometatarsal length 3; L_{tmt4} : tarsometatarsal length 4; L_{tmt5} : tarsometatarsal length 5; L_{med} : medial length; L_{lat} : lateral length; W_{prox} : proximal width; W_{mid} : middle width; W_{dist} : distal width; W_{toes} : width between toes.

Dimensions mesurées sur les empreintes de pieds expérimentales. L_{tot1} : longueur totale 1 ; L_{tot2} : longueur totale 2 ; L_{tot3} : longueur totale 3 ; L_{tot4} : longueur totale 4 ; L_{tot5} : longueur totale 5 ; L_{tmt1} : longueur tarsométatarsienne 1 ; L_{tmt2} : longueur tarsométatarsienne 2 ; L_{tmt3} : longueur tarsométatarsienne 3 ; L_{tmt4} : longueur tarsométatarsienne 4 ; L_{tmt5} : longueur tarsométatarsienne 5 ; L_{med} : longueur médiale ; L_{lat} : longueur latérale ; W_{prox} : largeur proximale ; W_{mid} : largeur du médiopied ; W_{dist} : largeur distale ; W_{toes} : largeur entre les orteils.

Of the 5 areal measurements, the first four (Area 1 to Area 4) correspond to products between footprint length and footprint width(s) (Fig. 4). The last area (A5) that was measured for 18 of the 20 participants corresponds to the precise footprint area determined only on the 3D models obtained by photogrammetry from Geomagic Studio 2012.

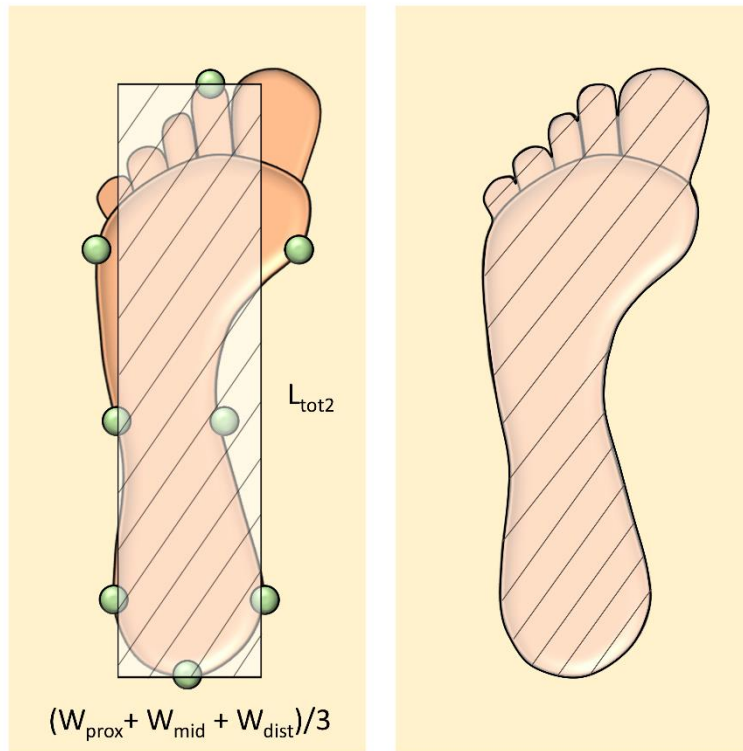
The photogrammetric models were also used to verify the measurements taken in situ. No significant differences were found for the 16 linear dimensions between the measurements taken in the field and those taken on the 3D models from Geomagic studio 2012 (Student's t-test: $P \gg 0.05$; mean deviation < 0.1 cm).



Area 1 (A_1)

Area 2 (A_2)

Area 3 (A_3)



Area 4 (A_4)

Area 5 (A_5)

Fig. 4. Area measured on the experimental footprints.

Superficies mesurées sur les empreintes de pieds expérimentales.

2.2.2. Correlation stature – footprint morphometrics

The correlation between the stature of the participants and the individual mean of each of the 21 morphometric variables was sought: the Pearson correlation coefficient and the linear regression equation giving the best prediction were calculated for each variable. The standard errors a and b for each equation are also given, “ a ” corresponding to the directing coefficient and “ b ” to the intercept of the equation $Y = ax + b$ where Y corresponds to the stature and x to the morphometric variable considered. The determination of the linear model and the different statistical parameters were obtained from the R software (R Development Core Team, v.4.1.3).

2.2.3. Intraindividual variation

Intraindividual variation was quantified for each individual and each variable using two parameters (Appendix B). The first is the coefficient of intraindividual variation, defined as the ratio between the individual mean of each variable and the intraindividual standard deviation of that variable. This coefficient of variation provides information on the average intraindividual variation of each variable.

The second parameter is the maximum intraindividual deviation from the individual mean of each variable. This parameter is particularly useful in determining the uncertainties when estimating stature on isolated prints.

These two parameters were not quantified for Area 5 determined on the photogrammetric models because their number per individual is too small.

3. Results

3.1. Correlation stature – footprint morphometrics

The morphometric variables of the footprints have highly variable correlations with stature (Fig. 5, Fig. 6, Fig. 7). Correlation coefficients range from 0.28 to 0.70 (Table 2). Lengths were the most correlated variables, especially for those associated with the first, second, and third toes, with less correlation for the fourth and fifth toes (Fig. 5; Table 2). Tarsometatarsal lengths had similar or even higher correlations than total lengths (Table 2). The correlation coefficients between stature and metatarsal lengths 1, 2, and 3 are extremely close ($r = 0.69$ – 0.70) which is also the case for total lengths 1, 2, and 3 ($r = 0.69$).

Widths correlated much less with stature (Fig. 6; Table 2). Proximal width ($r = 0.53$) and especially width between the toes (0.64) correlated more strongly with stature than midfoot width (0.39) or forefoot width (0.28).

The correlation coefficients of the areas have intermediate values between those of the lengths and those of the widths (Fig. 7; Table 2). The exact area A5 determined on the 3D models (Area 5) is the surface best correlated with stature ($r = 0.59$). On the contrary, the area A1 corresponding to the product between distal width (W_{dist}) and total length 2 ($L_{\text{tot}2}$) is the least correlated area ($r = 0.39$).

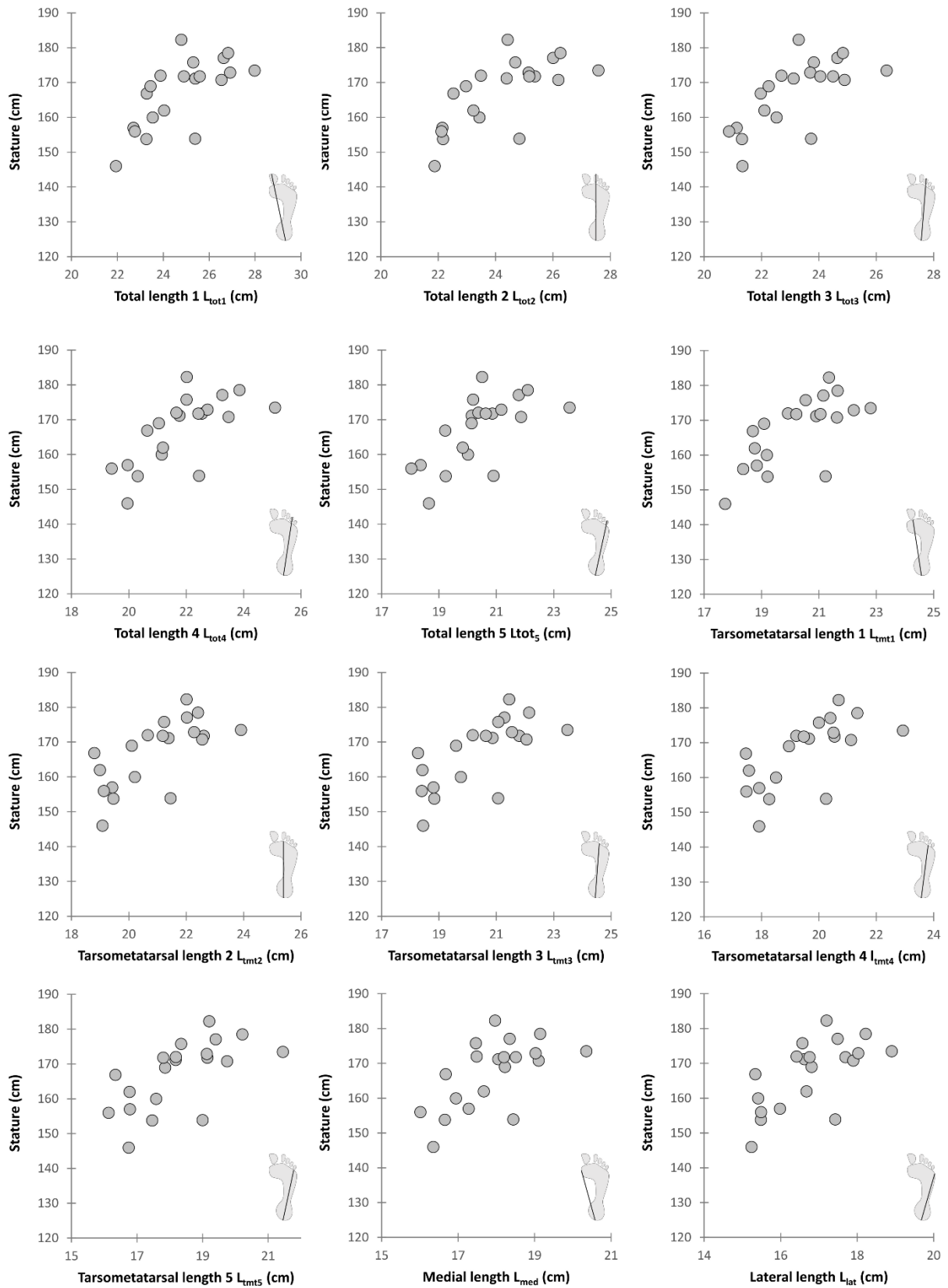


Fig. 5. Variation in stature and experimental footprint lengths.

Variation de la stature en fonction des longueurs des empreintes expérimentales.

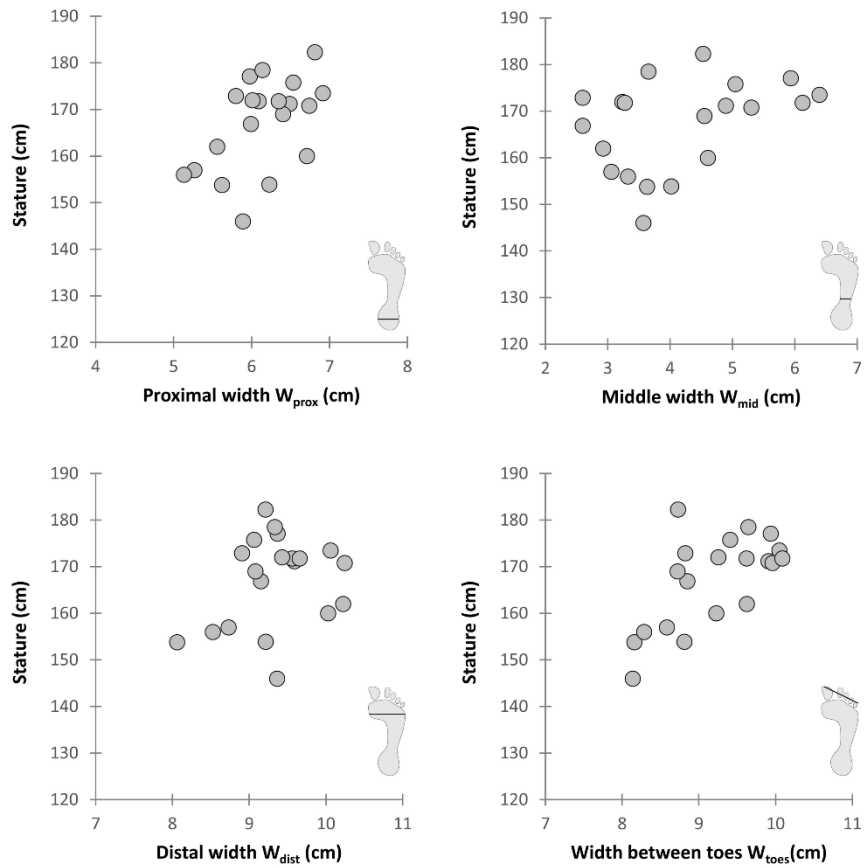


Fig. 6. Variation in stature and experimental footprint widths.

Variation de la stature en fonction des largeurs des empreintes expérimentales.

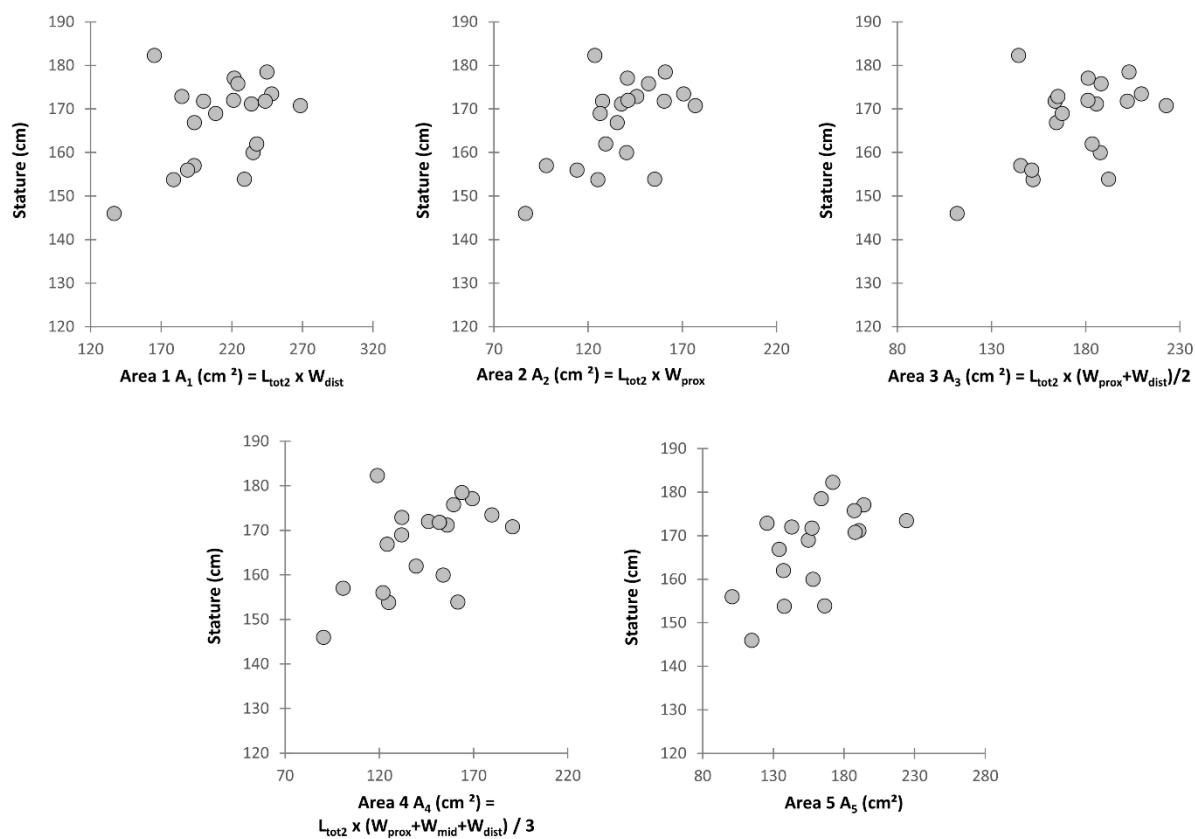


Fig. 7. Variation in stature and experimental footprint areas.

Variation de la stature en fonction des superficies des empreintes expérimentales.

Table 2. Correlation and linear regression equations between footprint morphometric variables and stature. Ltot1: total length 1; Ltot2: total length 2; Ltot3: total length 3; Ltot4: total length 4; Ltot5: total length 5; Ltmt1: tarsometatarsal length 1; Ltmt2: tarsometatarsal length 2; Ltmt3: tarsometatarsal length 3; Ltmt4: tarsometatarsal length 4; Ltmt5: tarsometatarsal length 5; Lmed: medial length; Llat: lateral length; Wprox: proximal width; Wmid: middle width; Wdist: distal width; Wtoes: width between toes.

Corrélation et équations de régressions linéaires entre les variables morphométriques des empreintes et la stature. Ltot1 : longueur totale 1 ; Ltot2 : longueur totale 2 ; Ltot3 : longueur totale 3 ; Ltot4 : longueur totale 4 ; Ltot5 : longueur totale 5 ; Ltmt1 : longueur tarsométatarsienne 1 ; Ltmt2 : longueur tarsométatarsienne 2 ; Ltmt3 : longueur tarsométatarsienne 3 ; Ltmt4 : longueur tarsométatarsienne 4 ; Ltmt5 : longueur tarsométatarsienne 5 ; Lmed : longueur médiale ; Llat : longueur latérale ; Wprox : largeur proximale ; Wmid : largeur du médiopied ; Wdist : largeur distale ; Wtoes : largeur entre les orteils.

Morphometric variables (x)	Number of individuals (N)	Pearson correlation coefficient (r)	Linear equation for estimating stature (y)	Standard error a	Standard error b
L _{tot1}	20	0.69	y = 4.1X + 66.9	1.0	24.7
L _{tot2}	20	0.69	y = 4.1X + 67.6	1.0	24.4
L _{tot3}	20	0.69	y = 4.5X + 62.5	1.1	26.0
L _{tot4}	20	0.68	y = 4.6X + 66.5	1.2	25.4
L _{tot5}	20	0.65	y = 4.8X + 70.1	1.3	26.1
L _{tmt1}	20	0.70	y = 4.8X + 70.6	1.2	23.6
L _{tmt2}	20	0.69	y = 4.5X + 72.5	1.1	23.7
L _{tmt3}	20	0.70	y = 4.5X + 75.8	1.1	22.2
L _{tmt4}	20	0.66	y = 4.3X + 83.1	1.2	22.5
L _{tmt5}	20	0.64	y = 4.5X + 85.6	1.3	23.5
L _{med}	20	0.62	y = 5.6X + 67.2	1.7	29.9
L _{lat}	20	0.65	y = 5.9X + 68.2	1.6	27.4
W _{prox}	20	0.53	y = 10.3X + 103.7	4.0	24.4
W _{mid}	20	0.39	y = 3.2X + 153.6	1.8	7.9
W _{dist}	20	0.28	y = 4.9X + 121.4	4.0	37.4
W _{toes}	20	0.64	y = 9.6X + 78.9	2.8	25.4
Area 1	20	0.39	y = 0.1X + 142.2	0.1	14.1
Area 2	20	0.56	y = 0.2X + 133.7	0.1	11.7
Area 3	20	0.48	y = 0.2X + 135.8	0.1	13.6
Area 4	20	0.52	y = 0.2X + 138.5	2.2	54.3
Area 5	18	0.59	y = 0.2X + 137.9	0.1	10.4

Therefore, lengths are the most reliable variables for predicting stature. Tarsometatarsal length can be a good surrogate for total length, especially for incomplete footprints.

4.2. Intraindividual variation

Lengths are the variables with the lowest coefficient of variation (Fig. 8; Table 3). The differences in average coefficients of variation between the different lengths are small (4.8–6.8%). The total length from the base of the heel to the tip of the second toe (L_{tot2}) is the variable with the lowest average coefficient of variation (4.9%). The widths show large coefficients of variation and are very different from one width to another (7.1–28.4%). The minimum width of the middle of the impression (W_{mid}) is the variable with the highest average coefficient (28.4%), the proximal width (W_{prox}) also has a high coefficient of variation (12.5%) whereas the distal width (W_{dist}) and the width between the toes (W_{toes}) have lower coefficients of variation (7.1% and 8.5% respectively) approaching that of the lengths (4.8–6.8%). Footprint areas also have high coefficients of variation and differ from one variable to another (10.7%–19.9%). Areas 2 to 4 have higher coefficients of variation (15.2–19.9%) than Area 1 (10.7%), which is consistent with the fact that they are calculated with the proximal width and in some cases the width of the middle of the footprint having very high coefficients of variation.

Similar but not completely identical trends are observed from the maximum intraindividual deviation from the individual mean (Table 3). The lengths have the lowest maximum deviations from the mean (13.4–21.4%). The total length from the base of the heel to the tip of the second toe (L_{tot2}) had the lowest deviation (13.4%). The widths have high deviations (20.7–92.3%) especially for the width of the middle of the footprint (W_{mid} , 92.3%). Finally, the areas are clearly the variables showing the largest deviations (85.8–87.4%).

These two dispersion parameters thus show that lengths, and in particular the length between the base of the heel and the tip of the second toe (L_{tot2}), are the morphometric variables with the least intraindividual dispersion and consequently the ones that will give the lowest uncertainties in the estimation of stature on isolated footprints.

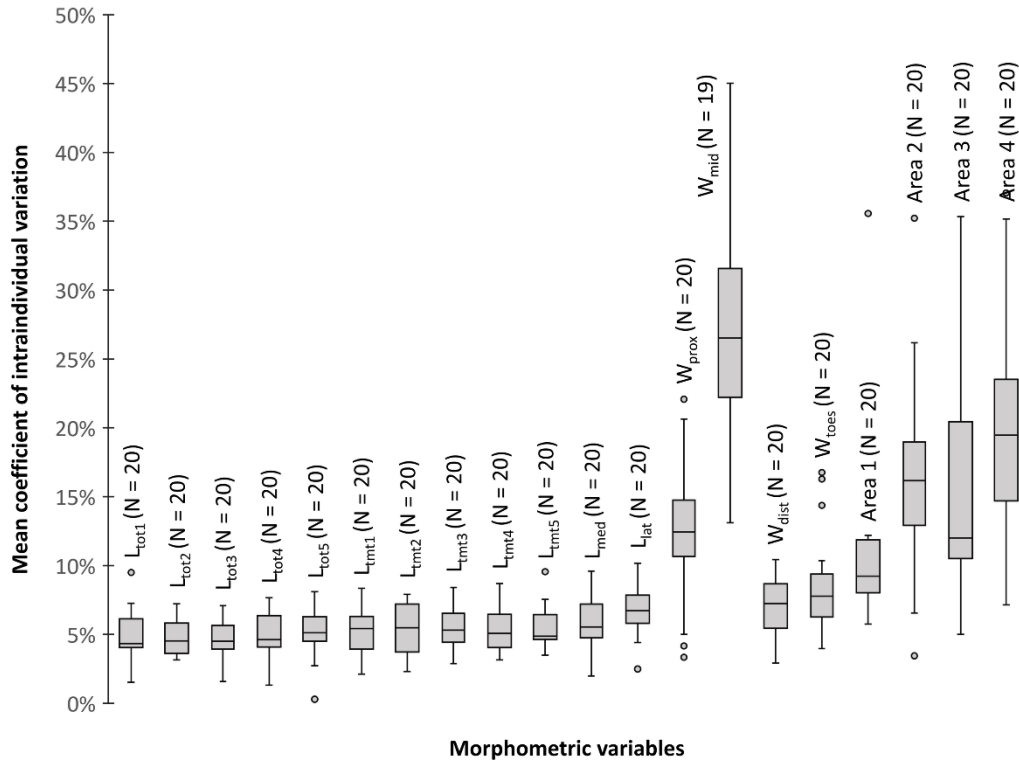


Figure 8: Variation of the coefficient of intraindividual variation according to the morphometric variables measured on the experimental footprints. L_{tot1}: total length 1 ; L_{tot2}: total length 2 ; L_{tot3}: total length 3 ; L_{tot4}: total length 4 ; L_{tot5}: total length 5 ; L_{tmt1}: tarsometatarsal length 1 ; L_{tmt2}: tarsometatarsal length 2 ; L_{tmt3}: tarsometatarsal length 3 ; L_{tmt4}: tarsometatarsal length 4 ; L_{tmt5}: tarsometatarsal length 5 ; L_{med}: medial length ; L_{lat}: lateral length ; W_{prox}: proximal width ; W_{mid}: middle width ; W_{dist}: distal width ; W_{toes}: width between toes.

Figure 8: Variation du coefficient de variation intraindividuel en fonction des variables morphométriques mesurées sur les empreintes expérimentales. L_{tot1} : longueur totale 1 ; L_{tot2} : longueur totale 2 ; L_{tot3} : longueur totale 3 ; L_{tot4} : longueur totale 4 ; L_{tot5} : longueur totale 5 ; L_{tmt1} : longueur tarsométatarsienne 1 ; L_{tmt2} : longueur tarsométatarsienne 2 ; L_{tmt3} : longueur tarsométatarsienne 3 ; L_{tmt4} : longueur tarsométatarsienne 4 ; L_{tmt5} : longueur tarsométatarsienne 5 ; L_{med} : longueur médiale ; L_{lat} : longueur latérale ; W_{prox} : largeur proximale ; W_{mid} : largeur du médiopied ; W_{dist} : largeur distale ; W_{toes} : largeur entre les orteils.

Table 3: Mean coefficient of intraindividual variation and maximum deviation from the mean for each morphometric variable measured on the experimental footprints. L_{tot1} : total length 1 ; L_{tot2} : total length 2 ; L_{tot3} : total length 3 ; L_{tot4} : total length 4 ; L_{tot5} : total length 5 ; L_{tmt1} : tarsometatarsal length 1 ; L_{tmt2} : tarsometatarsal length 2 ; L_{tmt3} : tarsometatarsal length 3 ; L_{tmt4} : tarsometatarsal length 4 ; L_{tmt5} : tarsometatarsal length 5 ; L_{med} : medial length ; L_{lat} : lateral length ; W_{prox} : proximal width ; W_{mid} : middle width ; W_{dist} : distal width ; W_{toes} : width between toes.

Tableau 3 : Coefficient de variation intraindividuel moyen et écart maximum par rapport à la moyenne pour chaque variable morphométrique mesurée sur les empreintes de pieds expérimentales. L_{tot1} : longueur totale 1 ; L_{tot2} : longueur totale 2 ; L_{tot3} : longueur totale 3 ; L_{tot4} : longueur totale 4 ; L_{tot5} : longueur totale 5 ; L_{tmt1} : longueur tarsométatarsienne 1 ; L_{tmt2} : longueur tarsométatarsienne 2 ; L_{tmt3} : longueur tarsométatarsienne 3 ; L_{tmt4} : longueur tarsométatarsienne 4 ; L_{tmt5} : longueur tarsométatarsienne 5 ; L_{med} : longueur médiale ; L_{lat} : longueur latérale ; W_{prox} : largeur proximale ; W_{mid} : largeur du médiopied ; W_{dist} : largeur distale ; W_{toes} : largeur entre les orteils.

Morphometric variables	Mean coefficient of variation (%)	Maximum deviation from the mean (%)
L_{tot1}	4.9%	16.9%
L_{tot2}	4.8%	13.4%
L_{tot3}	4.8%	14.6%
L_{tot4}	4.9%	14.0%
L_{tot5}	5.1%	16.5%
L_{tmt1}	5.3%	18.9%
L_{tmt2}	5.4%	15.3%
L_{tmt3}	5.5%	15.0%
L_{tmt4}	5.2%	15.9%
L_{tmt5}	5.4%	21.4%
L_{med}	5.8%	18.1%
L_{lat}	6.8%	15.3%
W_{prox}	12.5%	38.0%
W_{mid}	28.4%	92.3%
W_{dist}	7.1%	20.7%
W_{toes}	8.5%	34.4%
Area 1	10.7%	86.2%
Area 2	16.5%	85.8%
Area 3	15.2%	86.1%
Area 4	19.9%	87.4%

4. Discussion

4.1. Correlation stature – footprint morphometrics

The results of this experimental study showed that footprint lengths were the variables most correlated with stature. In addition to total lengths, tarsometatarsal lengths showed a significant correlation with stature. This variable may therefore be particularly useful when total length cannot be measured. Widths as well as areas have a lower correlation and therefore cannot provide reliable estimates of stature. However, they can be used to estimate other body characteristics such as the body mass for the areas (Dingwall et al., 2013, Bennett and Morse, 2014, Domjanic et al., 2015, Ruff et al., 2021).

This relationship between footprint length and stature should not be confused with that between foot length and stature. Indeed, the two relationships are different (Fig. 9), with footprints being on average longer (mean L_{tot2} : 24.2 cm) than associated feet (mean foot length: 23.3 cm). Such differences between footprint and foot length have been highlighted in previous studies (Dingwall et al., 2013) and justify the use of an experimental framework to estimate stature from footprints and not from foot length alone.

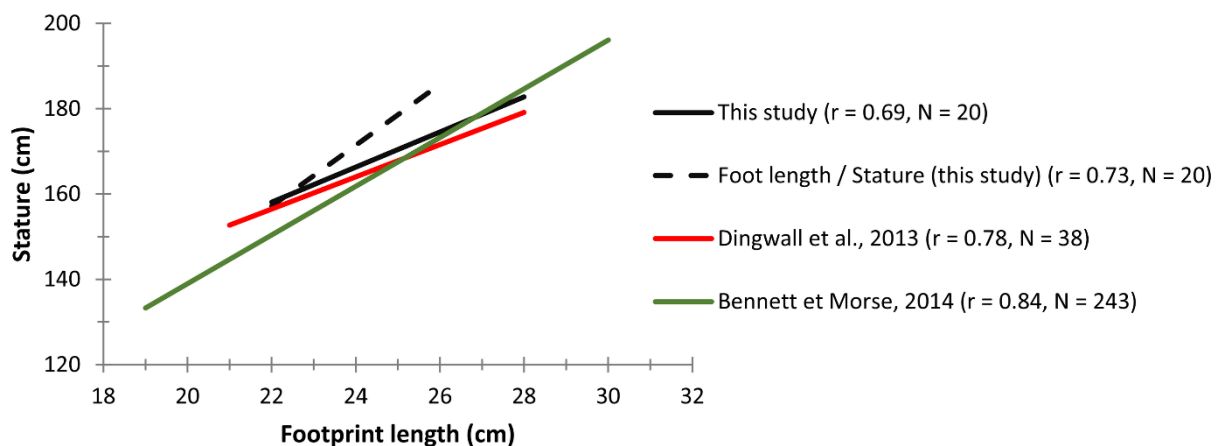


Fig. 9. Variation in stature and footprint length (measured between the base of the heel and the tip of the second toe) for different studies on experimental footprints made on sandy substrate.

Variation de la stature en fonction de la longueur des empreintes (mesurée entre la base du talon et l'extrémité du second orteil) pour différentes études sur des empreintes de pieds expérimentales réalisées sur des substrats sableux.

The relationship obtained for the total length 2 (L_{tot2}) is close to other relationships from experimental studies conducted in sandy substrates (Fig. 9). In particular, it is very close to that used by Dingwall et al. in 2013 in a study conducted on 38 usually unshod individuals. However, despite this closeness, these other experimental relationships show a stronger correlation than that obtained in this study (Fig. 9). This difference may possibly be related to variations in the nature of the substrates, for example in their rigidity or deformability impacting the morphological variation of the footprints. But it is more likely that it is related to the sample of individuals used in this study. Indeed, it is not only the correlation between footprint length and stature that is

weak, but also that between foot length and stature ($r = 0.72$). This greater uncertainty would therefore be related to the difference in the number of participants, as this exploratory study had a smaller number of individuals, and/or to the variation in body proportions that was greater in our sample.

Thus, length remains the variable most correlated with stature but the regression is linked to a significant residual uncertainty that must be taken into account. This regression and its uncertainty are only valid for this type of loose sandy substrate with fine to medium grain size, different relationships would exist for footprints made in other types of substrates (muddy, clayey...).

4.2. Intraindividual variation

This study also shows a strong intraindividual variation for different morphometric variables. The knowledge of this variation enables to quantify the uncertainties when estimating statures of isolated footprints that have not been associated within a trackway. One of the contributions of this experimental study is that it quantified intraindividual variation in variables other than length.

Lengths are the variables with the least intraindividual variation and thus the one to be preferred to minimize estimation uncertainties. Considering both the correlation between footprint morphometrics and stature as well as intraindividual variation, the total length between the base of the heel and the second toe (L_{tot2}) is the variable with the least uncertainty when estimating stature on an isolated footprint. However, even if the uncertainty is less than on the other variables, it remains important. Indeed, considering only the intraindividual variation, a stature estimated from the total length (L_{tot2}) of an isolated footprint is subject to an uncertainty of plus or minus 13.4% (corresponding to the maximum intraindividual deviation from the mean determined for this variable). Thus, if an isolated footprint has a total length equivalent to a stature of 170 cm, this print would have been made by an individual whose real height is between 147 and 192 cm. This high uncertainty raises questions about stature estimation for isolated fossil footprints that were left under similar substrate conditions (Duveau, 2021, Mayoral et al., 2021). Moreover, this uncertainty of 13.4% is only related to intraindividual dispersion and it is necessary to add to it the residual uncertainty of the regression between the average length of the footprints and the stature of the individuals.

However, these uncertainties due to intraindividual variation must be weighed because they are only valid in particular substrate conditions: loose and easily deformed sand. Even if several hominin footprints have been discovered in similar conditions, others have been left in different substrates such as clayey mud (Manolis et al., 2000, Onac et al., 2005, Citton et al., 2017, Ledoux et al., 2017) or volcanic ash (Leakey and Hay, 1979, Mietto et al., 2003, Masao et al., 2016, McNutt et al., 2021) having a lesser capacity for deformation; the footprints made in these substrates are morphologically closer to the anatomy of the foot and present a less important intraindividual dispersion.

4.3. From experimental relationships to fossil data

Apart from these uncertainties related to regression residuals and intraindividual variation, it is necessary to address the application of experimental relationships to fossil taxa. In paleoanthropology, stature estimation is very common and is not only performed from footprints but also from the dimensions of long bones (Ruff et al., 1997, Porter, 2002, Carretero et al., 2012). Such stature estimates give a picture of an extinct individual as a whole and not just the fragmentary skeletal remains that have been preserved. Variation in stature is also important in our understanding of human evolution. There is a trend toward increasing height during evolution even though this trend is not linear and there are exceptions such as recent small species (McHenry, 1991, Ruff et al., 1997, Brown et al., 2004). However, despite their importance in paleoanthropological research, estimates of stature and more generally of body characteristics, whether made on long bones or footprints, are subject to bias: the relationships used are defined in modern populations and not in fossil taxa in which the body proportions probably differed (Smith et al., 1996, Grabowski et al., 2015, Burgess et al., 2018, Walker et al., 2018).

This application bias does not only affect fossil species but is also valid in modern populations. First, within the same population, there is variation in the ratio of foot length to stature according to the age of the individual, as this ratio decreases during adolescence (Fig. 10). Yet this ontogenetic variation is rarely taken into account in stature estimates based on experimental footprints, as most participants in these studies are adults (Dingwall et al., 2013, Bennett and Morse, 2014, Wiseman and De Groote, 2022). There is also variation in the foot length to stature for individuals of the same age class but from different populations (Appendix C). An interesting parameter to study in this context concerns the habitual wearing of shoes. Indeed, several studies have shown that the morphology of the foot, and in particular that of the arch of the foot, can be affected by whether or not an individual is used to wearing shoes (Ashizawa et al., 1997, D'Août et al., 2009, Hollander et al., 2017). Such morphological changes could impact the relationship between foot length and stature and thus bias the estimates from footprints since the experiments, with a few exceptions (Dingwall et al., 2013, Ruff et al., 2021), are conducted on individuals who are usually shod, which was not the case for fossil hominin taxa. However, comparison of the ratios of foot length to stature show that this ratio in usually unshod individuals is included within the variation of usually shod individuals (Appendix C).

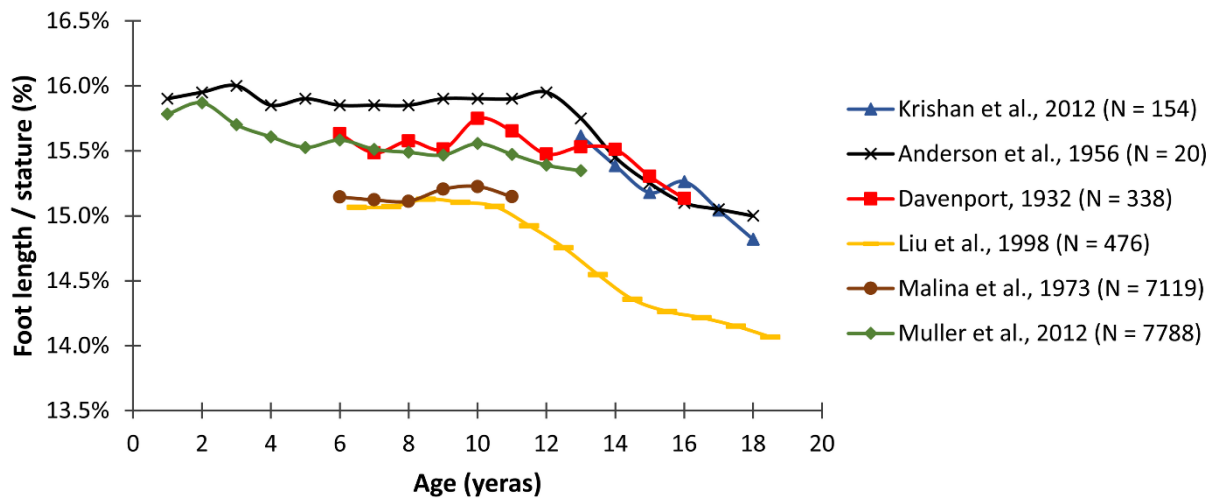


Fig. 10. Foot length to stature ratio vs. age in different modern populations (Anderson et al., 1956, Davenport, 1932, Krishan et al., 2012, Liu et al., 1998, Malina et al., 1973, Müller et al., 2012).

Variation du rapport entre la longueur du pied et la stature et l'âge pour différentes populations modernes (Anderson et al., 1956, Davenport, 1932, Krishan et al., 2012, Liu et al., 1998, Malina et al., 1973, Müller et al., 2012).

If the relationship between foot length and stature varies between different modern populations, it is possible that it also varies between *Homo sapiens* and fossil hominin taxa. Indeed, body proportions, such as the intermembral index or the crural index differ between species (Richmond et al., 2002, Polk, 2004, Jungers, 2009, Tallman, 2013). However, the fossil record is fragmentary and the foot length to stature ratio is unknown in all fossil hominin taxa, including the well-known Neandertals. Only estimates of this relationship have been made from anatomical reconstructions of composite feet and stature estimates made on long bones (Table 4). According to these estimates, there is a variation in this ratio between taxa. In *Australopithecus afarensis* (Lucy), this ratio would be slightly larger (15.4–16.2%) than the average ratio of modern populations (mean: 14–15%). In *Homo floresiensis*, it is more important (18.0%) than that of modern populations. Finally, the ratio of Neandertals is close to that of modern populations although the range of estimates is large (12.7–15.4%). It should be noted, however, that these estimates are also subject to biases in both reconstruction and stature estimation from long bones. Therefore, they cannot be considered totally reliable. This relationship between foot length and stature is not completely available in fossil species but it is known in non-human primates and in particular in the bonobo, our closest relative within the Hominoidea with the common chimpanzee. In bonobos, this ratio varies between 17 and 20% with an average of 18.8% (Coolidge and Shea, 1982). It is therefore likely that the ratio between foot length and stature between the different hominin species does not differ more than between modern humans and bonobos.

Table 4. Estimated foot length to stature ratio for different fossil hominin taxa after anatomical reconstructions.

Estimation du rapport entre la longueur du pied et la stature pour différents taxons d'hominines fossiles après reconstructions anatomiques.

Taxon		Foot length	Stature	Foot length-stature ratio	References
<i>Australopithecus afarensis</i>	AL288-1	16.5-17.3 cm	106.7	15.4-16.2%	[81-82]
<i>Homo floresiensis</i>	LB1	19.1 cm	106	18.0%	[62, 83]
<i>Homo neanderthalensis</i>	La Ferrassie 1	24 cm	168-173 cm	13.9-14.2%	[60, 84]
<i>Homo neanderthalensis</i>	La Ferrassie 2	20.0 cm (right foot) - 20.5 cm (left foot)	146-157 cm	12.7-14.0%	[60, 84]
<i>Homo neanderthalensis</i>	Kiik-Koba	24.8 cm (right foot) - 24.7 cm (left foot)	161 cm	15.3-15.4%	[60, 84]

To summary, the variation in the relationship between foot length and stature between different hominin species is not known precisely but is likely adding a new uncertainty to the estimation of statures from footprints in addition to that related to the residuals of experimental regressions and intraindividual variation.

6. Conclusion

This exploratory experimental study showed that among a set of morphometric variables, footprint lengths were the most correlated with individual stature. They were also the variables with the least intraindividual variation. More precisely, the total length from the base of the heel to the tip of the second toe is the variable with the least uncertainty when estimating stature. In addition, this study showed that when total lengths could not be measured due to lack of completeness, other variables such as tarsometatarsal length could be used.

However, the estimation of stature from footprints is uncertain, especially for isolated footprints. It is indeed linked to three types of uncertainties: the residuals of the linear regression between footprint length and stature, the intraindividual variation that can be very important in the case of very deformable soft substrate, and the variations in body proportions within the different populations and between the different fossil taxa.

This study is exploratory and it will be necessary to increase the number of individuals, incorporating in particular young individuals in which the ratio between foot length and stature may differ from that of the adult, but also to conduct experiments on a wide variety of substrates (clays, sand, mud...). It will thus be possible to quantify different relationships and their uncertainties for each type of site where fossil footprints have been discovered and thus specify the paleobiological estimates on this vestige so particular in paleoanthropology.

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Appendices A, B, C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anthro.2022.103067>.

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