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New interpretation of Laetoli footprints using an experimental approach and Procrustes analysis: Preliminary results

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Abstract

We compared Laetoli footprints (G1/35-36-37, G3/26) with modern humans (62 footprints), and a chimpanzee walking bipedally (five footprints). Video cameras allowed us to capture walking parameters on a wet clay walkway, and the Procrustes method was used to analyze the footprint shape (outlines and centres of pressure). Like humans, Laetoli hominids walked with small feet gap, and probably low velocity (they used heels as brakes). They preserved certain ape-like traits (foot proportions, roll-off). They also possessed more marked human-like traits (small vault, metatarsal pressure, similar toe-off). Like humans walking on a soft ground, they flexed toes at ground contact, and then propelled themselves by pushing on the ball of the foot and on digits (hallux and lateral toes acting together). The hypothesis of permanently flexed, or curled-underneath, digits was not retained by comparison with the chimpanzee. ***To cite this article: C. Berge et al., C. R. Palevol 4 (2005)***.

Résumé

Nouvelle interprétation des empreintes de pas de Laetoli utilisant l'approche expérimentale et l'analyse procuste : résultats préliminaires. Nous comparons les empreintes de pas de Laetoli (G1/35-36-37, G3/26), avec celles des humains (62 empreintes), et d'un chimpanzé marchant en bipédie (cinq empreintes). Des cameras vidéo servent à enregistrer les paramètres de la marche sur une piste d'argile molle, et la méthode procuste est utilisée pour analyser la forme des empreintes (contours et centres de pression). Comme les humains, les hominidés de Laetoli marchaient avec un espace faible entre les pieds et probablement une faible vitesse (ils freinaient avec les talons). Ils avaient conservé des caractères rappelant les grands singes (proportions et roulé du pied vers l'extérieur). Ils possédaient aussi, de façon plus marquée, des caractères de type humain (petite voûte plantaire, pression sur les métatarses, même levé des orteils). Comme les humains sur un sol mou, ils fléchissaient les orteils au contact du sol, puis se propulsaient en poussant sur les pelotes plantaires et sur les orteils (hallux et doigts latéraux fonctionnant

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ensemble). L'hypothèse d'orteils fléchis de façon permanente, ou repliés sous le pied, n'a pas été retenue par comparaison avec le chimpanzé. ***Pour citer cet article : C. Berge et al., C. R. Palevol 4 (2005)***.

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Mots clés : Bipédie ; Morphométrie ; Laetoli ; Australopithecus ; Pan ; Homo

1. Introduction

In 1978, the discovery of hominid tracks at Laetoli (Tanzania) revived the debate about bipedal abilities in early hominids. Fossil traces found in Tuff 7 at Site G were rapidly attributed to hominids because of their humanlike appearance [7,8,16,19,36]. The Laetoli site comprised numerous Pliocene fossils, including *Australopithecus* remains and was dated to around 3.6 Myr [35,36]. At first sight, hominid footprints at Site G suggest parallel trails made by two individuals: a smaller and a larger one, which walked with no deviation on a distance of 25 m [8]. However, after more excavation, M.D. Leakey [19] described three individuals: a track of a single individual (G1) and two superimposed tracks made by two individuals passing in succession (G2 and G3). Hominids walked on a large and flat surface formed by a thick bed of damp and very cohesive ash that had been deposited during an eruptive episode [20,36]. M.D. Leakey [19] listed a total of 39 hominid footprints for G1, and 31 for the dual one. The substrate is now solidified tuff. Unfortunately, most prints were damaged or still incompletely excavated when they were reburied. Only casts of sections of tracks are now available.

Descriptions of Laetoli footprints have given rise to various taxonomical and functional interpretations. For some authors, the Laetoli footprints are close to human ones [12,29–31,33]. Tuttle et al. [31,32] suggested that Laetoli footprints may correspond to a species of the genus *Homo* who lived contemporaneously with *A. afarensis*. On the contrary, for others, the foot skeleton of *A. afarensis* (Hadar) shows a better fit than the human foot [26,27,36]. However, such interpretations depend on fossil-foot-bone reconstruction. White and Suwa [36] reconstructed the australopithecine (Hadar) foot with human-like traits (short and rectilinear toes, adducted hallux, medial longitudinal arch), whereas Susman [27,28] considered the Hadar foot morphology to be the result of combined ape-like and human-like traits. Clarke [8,9] reconstructed the australopithecine foot (Sterkfontein, 3.6 Myr) with an ape-like morphology (long, curved toes and a diverged hallux). Stern and Susman [26] suggested that many steps in the Laetoli hominids, as in the chimpanzee, were characterized by a curling of lateral toes. They asserted that body weight was not transferred (or differently transferred) to the medial part of the foot (ball of the foot) as it is in humans at the end of stance phase. Clarke [8] agreed with Deloison [13,14] and proposed a list of ape-like traits observed in Laetoli footprints, such as weight-bearing on the lateral side of the foot, prominent medial expansion of the abductor hallucis muscle, pointed heel, and absence of individual toe impressions apart from the hallux. They concluded that the Laetoli hominids walked with curled-underneath digits. Clarke [8] added that this ape-like trait is consistent with the indication of arboreality seen in the australopithecine foot bones he studied.

The aim of this study is to reconsider Laetoli footprints in a more functional viewpoint with the use of the Procrustes method. We have attempted to reconstruct conditions close to those of Laetoli for modern humans and a chimpanzee walking bipedally. As body weight transfer and footfall differ in humans and chimpanzees, we analyzed them separately, by comparing Laetoli either with humans or with the chimpanzee. Because our preliminary study comprises a small number of fossil and chimpanzee prints, we only discuss reliable results in terms of functional significance and statistics.

2. Material and methods

2.1. Material

The fossil material comprises the cast section of tracks G1, G2, and G3. Three prints of G1 (37, 36, 35)

Table 1
Eighteen homologous landmarks defined in human and fossil prints, and applied to the chimpanzee prints
Tableau 1
Dix-huit points homologues définis sur les empreintes humaines et fossiles, et appliquées aux empreintes du chimpanzé. [a]: points manquants chez le chimpanzé.

No.	Definition
1	Heel, posterior edge (on foot symmetrical axis)
2	Heel, internal edge (at the level of landmark 13)
3	Sole, internal edge (at minimal breadth)
4	Metatarsus, internal edge (at maximal breadth)[a]
5	Hallux, metatarsus head[a]
6	Hallux, extremity
7	Hallux-toe II, metatarsus interval[a]
8	The lateral toe closest to hallux
9	Toe V, extremity
10	Toe V, Metatarsus head
11	Plant, external edge (at minimal breadth)
12	Heel, external edge (at the level of landmark 13)
13	Heel, centre of pressure (deepest point)
14	Sole, centre of pressure (deepest point between landmarks 3–11)
15	Hallux, metatarsus centre of pressure (deepest point)[a]
16	Toes II-V, metatarsus centre of pressure (deepest point)
17	Hallux, phalange centre of pressure (deepest point)
18	Toes II-V, phalange centre of pressure (deepest point)

[a] lacking in chimpanzee.

and one print of G3 (26) were used for geometric morphometry.

The living material comprises the tracks of nine adult humans (four males, five females) of European origin, and the track of one adult female chimpanzee (Table 1). The chimpanzee (Tiby, 14 years old, 45 kg) is a hybrid of *Pan paniscus* (father) and *P. troglodytes* (mother). The animal was born in captivity, lives with humans and other chimpanzees (Kino's Circus) and adopted a permanent bipedalism during experiment. In total, 62 human prints, and five chimpanzee prints have been measured. Because of the small number of fossil prints (4), we reduced the human sample to 9 prints (one per individual) to have a mean shape (consensus) that is intermediary between humans and fossils. We calculated two possible shapes for each fossil print and we found that differences in shape between two data captures were negligible in multivariate space.

2.2. Experiment

The walkway (length: 5 m; breadth: 45 cm; height: 4 cm) was made of thin wet clay. We maintained constant humidity to obtain a print depth comparable to those made in Laetoli ground. Measurement for ground density is not available because print depth also depends on individual characteristics, such as velocity, body weight, body proportions, sex, and peculiar type of foot stance. In human experiment, a video camera (24 frames/s) was placed perpendicular to the long axis of the walkway at a distance of 3.5 m (lateral view of two strides). In chimpanzee experiment, three wide angle video cameras (24 frames/s) were situated at 3.5, 6, and 4 m, to obtain lateral, posterior and superior views of the complete walkway respectively. We experimented with five or six consecutive trails to try to obtain different types of walk (but to no avail). As previously noticed in *Pan paniscus* [34], footfall pattern is relatively stable for each individual, with some differences between right and left feet. Finally, we retained a trail with five measurable footprints, i.e. with hallux and lateral-toes contact. Other prints with no toes contact were used for observation and other calculations.

2.3. Functional measurements

For each individual, we calculated hindlimb length (greater trochanter to heel contact), stride velocity, stride length (stride: between two initial heel contacts of the same foot), stride length relative to hindlimb length, foot angle (between foot symmetrical axis and track direction), feet gap (between two successive heel posterior landmarks measured perpendicularly to the track direction), and Froude number (Table 1). The Froude number (*Fr*) allows us to compare gaits in terms of dynamic similarity [2,3,25]. Calculation is the following one: $Fr = V^2 g^{-1} L^{-1}$, where V is velocity during one stride, g gravitational acceleration, and L hindlimb length.

Hindlimb length was measured at heel contact on films. Hindlimb was extended in humans, and flexed in chimpanzee [see also 11]. For Laetoli, we calculated an approximate hindlimb length from the femur length of *Australopithecus afarensis* Lucy (AL 288), considering that australopithecines had an extended hindlimb at heel contact, and a knee-to-foot/ femur ratio similar to humans [4,5].

2.4. Print measurements

Eighteen homologous landmarks have been defined in humans and Laetoli (Table 1, Fig. 1). Twelve of them

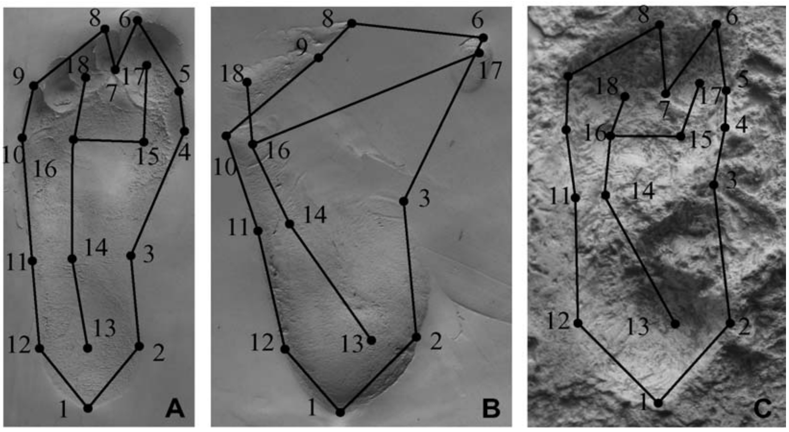

Fig. 1. Homologous landmarks defined in footprints. (A) *Homo* (18 landmarks); (B) *Pan* (14 landmarks); (C) Laetoli G1–37 (18 landmarks). Footprints outlines: landmarks 1 to12; centres of pressure: landmarks 13 to 18 (successive order drawn from films).
Fig. 1. Points homologues définis sur les empreintes de pas. (A) *Homo* (18 points) ; (B) *Pan* (14 points) ; (C) Laetoli G1–37 (18 points). Contours des empreintes : points 1 à 12 ; centres de pression : points 13 à 18 (ordre successif tracés à partir des films).

draw the outline of prints (landmarks 1 to 12), and six (landmarks 13–18) body weight transfer. Because the shape of prints is very different in our chimpanzee, the number of landmarks was reduced to 14 for the chimpanzee comparison (Table 1). Landmarks were digitalized with the 3D Revpro DX Microscribe (precision: 0.1 mm).

2.5. Statistics

Two analyses were carried out from Laetoli prints, comparing them either with humans (18 landmarks), or with the chimpanzee (14 landmarks). For each analysis, and after Procrustes superimposition, a principal-component analysis was computed from Procrustes residuals. We calculated the discriminant vector that best separates the two groups (Laetoli vs. humans, Laetoli vs. chimpanzee) in the multivariate space of shape (see [6,23,24]). Shape changes along discriminant vectors may be viewed in three planes: horizontal, sagittal and frontal. Here they are given in horizontal plane (superior view of prints) and sagittal plane (lateral view of prints). To compare distances from Laetoli to humans and from Laetoli to chimpanzees, we computed an additional Laetoli-humans analysis with 14 landmarks, and we calculated the Mahalanobis D^2 in the two 14-landmark analyses. Superimposition, graphics, parametric tests were calculated with APS Software [22], and D^2 with Matlab 5.3.

3. Results

3.1. Parameters of bipedal gait

Bipedal gait on a soft ground leads to various styles of walk in humans (Table 2). Froude numbers vary from 0.01 to 0.25, indicating that there is no real dynamic similarity (velocity is not proportional to hindlimb length) within humans walking in such conditions. Stride length relative to hindlimb length is also very variable (SL/HL: 120.0 to 166.7). In comparison to humans, the chimpanzee walked with a very large stride length, high relative velocity, and consequently a large Froude number (see other locomotor parameters in [1,10,17,18,21]). In proportion to its short (and flexed) hindlimb, stride is particularly long (SL/HL: 218.2). Similar values have been measured in *Pan paniscus* walking in normal conditions of bipedalism [1]. On the contrary, stride was very short in Laetoli printmakers. When associated to Lucy hindlimb reconstruction, Laetoli stride length turns out to be very human-like in proportions (SL/HL: 137.5).

There is considerable difference between humans and chimpanzees in the way body weight is displaced during bipedal walk (Table 2). The orthograde bipedal walk of humans is characterized by a reduced displacement of body weight from one supporting foot to the other, with reduced rotational movements of pelvis and shoulders around the vertebral column, and alternate arm swinging. In soft ground as here, we observed that

Table 2
Bipedal gait parameters for humans, chimpanzee, and Laetoli. HL: hindlimb length; SL: stride length; *V*: stride length velocity.* G1 (35-37) and data reconstructed from Hadar femur (AL288), see methods
Tableau 2
Paramètres de la marche bipède des humains, du chimpanzé et de Laetoli. HL : longueur du membre inférieur ; SL : longueur de l'enjambée ; *V* : vitesse de l'enjambée ; * : G1 (35-37) et données reconstituées à partir du fémur de l'Hadar (AL 288) ; voir méthodes. *Foot angle* : angle entre l'axe de symétrie du pied et la direction de la piste ; *feet gap* : espacement des deux pieds.

Specimens	Sex	*V* ($m\ s^{-1}$)	SL (m)	HL (m)	SL/HL (%)	*V*/HL (%)	Froude number	Foot angle (°)	Feet gap (cm)
Homo 1	M	0.75	1.22	0.85	143.5	88.2	0.07	15	9.3
Homo 2	M	1.17	1.37	0.92	148.9	127.2	0.15	14	0.2
Homo 3	M	1.50	1.25	0.93	134.4	161.3	0.25	21	4.5
Homo 4	M	0.81	1.08	0.85	127.1	95.3	0.08	21	9.0
Homo 5	F	0.71	1.09	0.84	129.8	84.5	0.06	16	0.4
Homo 6	F	0.77	1.26	0.86	146.5	89.5	0.07	5	1.1
Homo 7	F	1.16	1.40	0.84	166.7	138.1	0.16	8	0.7
Homo 8	F	0.72	1.08	0.90	120.0	80.0	0.06	9	9.4
Homo 9	F	0.32	0.79	0.78	101.3	41.0	0.01	6	0.8
Pan sp	F	0.96	0.96	0.44	218.2	218.2	0.21	11	30.8
Laetoli*	F?	—	0.88	0.64	137.5	—	—	21	3.9

stride lengths and velocity may vary greatly, although body weight transfer is relatively invariant. In humans, foot contact begins with the heel, continues with lateral edge of foot, instantly followed by metatarsal heads of digits (ball of the foot) and extremities of digits (hallux and lateral toes). Digits act together at ground contact and toe-off. At ground contact on a soft subtract, human digits are flexed. At toe-off, human digits are passively hyperextended under the effect of body weigh although they are submitted to flexor muscles (the muscles flexors digitorum and hallucis proprius are strongly stretched). On a soft ground, humans energetically push on hallux and lateral toes to propel themselves.

In our chimpanzee experiment, the walk in soft ground was not very different from descriptions of normal walks made on hard ground [1,10,11,15,17,34]. The chimpanzee walked with feet apart, high velocity, and wide stride lengths (Table 2). We observed on films that stride length is increased by the forward displacement of the supporting hip. Body weight is strongly laterally displaced alternately on each supporting foot, with wide swinging movements of arms in the opposite direction, and without movements of shoulders and head. Initial contact of the foot with the ground begins with the heel. Roll-off involves displacement of the centre of pressure along the lateral edge of the foot, down to the 5th metatarsal head. Then, later, the centre of pressure shifts towards the extremity of the hallux. In some cases observed here, foot contact stopped after lateral edge of mid-foot, digits leaving no print on the ground. At foot-off, the chimpanzee preserves flexed or curled-underneath toes, the propulsive force being generated mainly by heel and midfoot. Here toe-off is very variable (hallux first or hallux and lateral toes simultaneously or lateral toes first).

3.2. Laetoli footprints as compared with the human prints

The Procrustes analysis uses 18 homologous landmarks to compare Laetoli with human footprints. Calculation of a discriminant vector between humans and fossils indicates that the two patterns are clearly different ($R^2 = 0.95$, $F = 41.6$, $p < 2 \times 10^{-5}$, with 4 PC). Fig. 2 gives the coordinates of specimens in terms of shape differences and multivariate size. Prints of G1 (35-36-37) and G3 (26) have a similar shape but different sizes. As compared with the consensus (mean shape), humans show a narrow footprint characterized by a marked narrowing at midfoot, closer hallux and toe II, and lateral toes shorter than the hallux (Fig. 3A). Centres of pressure are aligned from heel to lateral toes. The distance between the hallux centre of pressure and the lateral-toes centre of pressure is short, not only because toe II and hallux are close together, but also because the maximal pressure corresponding to the lateral-toes falls frequently on toe II (sometimes between toe II and III; in

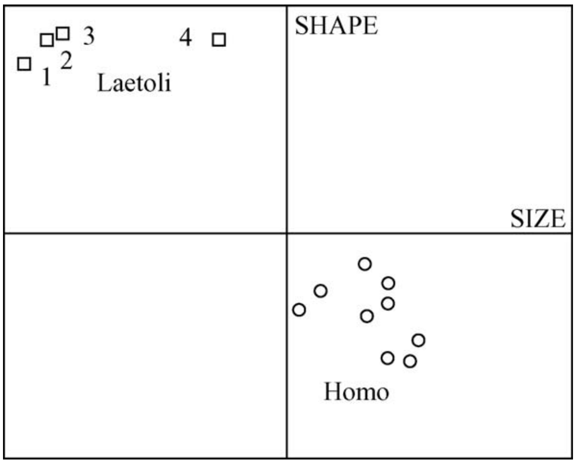

Fig. 2. Size and shape differences between Laetoli and human footprints. Shape: discriminant vector; size: centroid size (multivariate size) calculated from four PC (see text). The consensus (mean shape) is situated at *x*-axis and *y*-axis origin. **1**: G1-37; **2**: G1-36; **3**: G1-35; **4**: G3-26. G1 and G3 (same shape, different sizes) are strongly discriminated from humans.

Fig. 2. Différences de taille et de conformation entre les empreintes de Laetoli et des humains. *Shape* : vecteur discriminant ; *size* : taille centroïde (taille multivariée) calculés à partir de quatre CP (voir texte). Le consensus (conformation moyenne) est situé à l'origine des axes. **1**: G1-37 ; **2** : G1–36 ; **3** : G1-35; 4: G3-26. G1 et G3 (même conformation, différentes tailles) sont fortement discriminés des humains.

one case on toe IV). In lateral view, the plantar vault is well-marked (landmark 14 higher than landmarks 13, and 15–16). Body weight pressure is more marked at the level of metatarsal heads (ball of the foot), and digit extremities (hallux and lateral-toes centres of pressure) than at the level of the heel. Laetoli footprints display the opposite shape (Fig. 3B). In superior view, the print is very broad with no narrowing at midfoot, separated hallux and toe II, and lateral toes longer than hallux. The successive centres of pressure indicate that body weight pressure is internal at heel contact, then laterally displaced to the external edge of the foot and toes. We also observe that pressure on metatarsal heads is proportionally lower situated, and pressure on hallux and lateral toes more spaced than in humans. The lateral view of the print indicates that fossils had a small plantar vault, with a stronger pressure on heel than on metatarsal heads. Pressure was smaller on hallux and lateral toes than in humans. In frontal view (not represented here), lateral toes left a deeper print in the ground than hallux, whereas it is generally the reverse in humans.

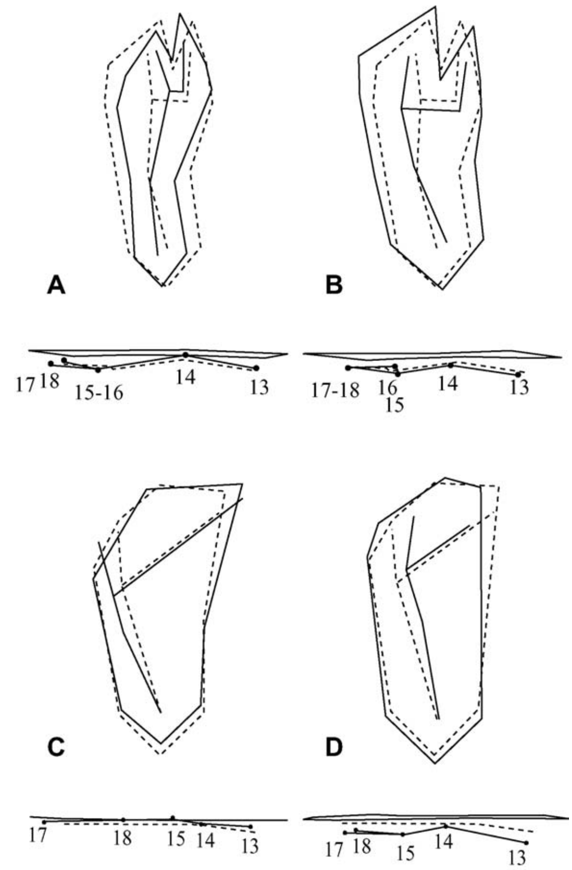

Fig. 3. Shape differences in footprints calculated from discriminant vectors (superior and lateral views). **A**–**B**: Comparison between *Homo* (**A**) and Laetoli (**B**) with 18 landmarks, 13 specimens; **C**–**D**: comparison between *Pan* (**C**) and Laetoli (**D**) with 14 landmarks, 9 specimens. In superior view, Laetoli differs from humans by footprint proportions and roll-off. In lateral view, Laetoli is close to humans, with a small vault, and metatarsal and toes pressure suggesting a human-like toe-off. See landmarks numbers in Fig. 1 and Table 1.

Fig. 3. Différences de conformation sur les empreintes calculées d'après les vecteurs discriminants (vues supérieures et latérales). **A**–**B** : Comparaison entre *Homo* (**A**) et Laetoli (**B**) à partir de 18 points, 13 spécimens ; **C**–**D** : comparaison entre *Pan* (**C**) et Laetoli (**D**) à partir de 14 points, 9 spécimens. En vue supérieure, Laetoli diffère des humains par les proportions de l'empreinte et le roulé du pied (appui interne puis externe). En vue latérale, Laetoli est proche des humains, avec une petite voûte plantaire, et une pression sur les métatarses et les orteils suggérant un levé des orteils de type humain. Voir les numéros des points sur la Fig. 1 et le Tableau 1.

3.3. Laetoli footprints as compared with the chimpanzee prints

The Procrustes analysis uses 14 homologous landmarks to compare Laetoli with the chimpanzee footprints. Discrimination is very high ($R^2 = 0.99$, $F = 311.6$, $p = 10^{-6}$ with 2 PC). In comparison to the consensus, the chimpanzee footprint is much larger at the level of digits than at the level of heel (Fig. 3C). The chimpanzee walked with flexed or curled-underneath toes, which are superimposed on the lateral edge. Thus, maximal pressure corresponding to lateral toes is on phalanges 1 or 2 of toe V, placed above toe extremity. Centres of pressure from heel to lateral toes are situated on the lateral edge of the foot. The hallux centre of pressure is further from lateral toes' centre of pressure. In lateral view, the print of the chimpanzee has no plantar vault. Only heel print is deep, sometimes hallux extremity. In comparison, the Laetoli footprint is narrower at the level of digits (Fig. 3D). Body weight transfer is much more internal from midfoot to toes' extremities. Hallux and lateral-toes centres of pressure are close together. In lateral view, the print is not completely flat as in the chimpanzee but indicates the presence of a vault with a marked pressure at the level of metatarsal heads (ball of the foot) and extremities of digits (hallux and lateral toes).

3.4. Laetoli close to humans or to the chimpanzee?

We calculated the Malahanobis D^2 with 4 PC in the two 14-landmark analyses (Laetoli-humans, Laetoli-chimpanzee). The distance between Laetoli and humans corresponds to $D^2 = 95.4$, whereas the distance between Laetoli and chimpanzee corresponds to $D^2 = 615.7$, that is to say six times more distant from the chimpanzee than from humans. In Table 2, gait parameters seem to increase the likeness between Laetoli hominids and modern humans. Contrary to the chimpanzee, Laetoli hominids walked with small stride lengths (absolute and relative measurements), and close feet.

4. Discussion

When describing Laetoli footprints, Clarke [8] concluded that the fossils reveal ape-like traits in their morphology and footfall. His opinion is reinforced by footprints made by two chimpanzees walking bipedally in wet sand. We can see in photographs given in Clarke [8 (p. 480)] that chimp prints were more human-like than in our experiment, the complete sole being printed on the ground, and sometimes hallux close to toe II. These prints indicate that the chimpanzees walked with the feet completely flat on the ground and extended toes, in which the distal phalanges touch the ground with their plantar surfaces. For Vereecke et al. [34], such a footfall corresponds to an interindividual variation. On the other hand, Clark [8] supported the idea that Laetoli hominids could walk with permanently curled-underneath toes (i.e. toes extremities under the first phalanges, from initial heel contact to toe-off). We believe that there is no intermediary footfall pattern in chimpanzees that may be used to put forward a hypothetical pattern for Laetoli hominids. In chimpanzees, either the supporting foot lands on the lateral edge with flexed or curled-underneath toes, or the supporting foot is flat on the ground with extended toes. In our experiment, for example, the chimpanzee always walked on the lateral edge of the foot, with flexed toes for right foot, and curled-underneath toes for left (Fig. 4A and B). Other chimpanzees observed in Kino's Circus, or described in literature, walked with flat feet and extended toes. In both cases, they cannot vary their footfalls [34]. In the first case, body weight pressure just before toe-off is on hallux (except when there is no hallux ground contact), but never on toes II–IV, which are flexed under toe V. In the second case, body weight exerts a reduced pressure on all the digits gathered together at ground contact. Laetoli Hominids walked with feet completely flat on the ground. Deep toe-prints indicate that body-weight pressure was very strong on digits acting together at ground contact and toe-off. In our experiment, most humans flexed toes at ground contact (toes extremities in contact with the ground and close to the ball of the foot) to increase friction, and extended them at toe-off (Fig. 4C). Hyperextension of digits creates adherent zones like small cupules, which are generally visible in first phalanges prints. R.J. Clarke found such cupules in the original moulds he made of the fossils, but he interpreted them as the marks of the extremities of curled-underneath digits (pers. commun.). Our present purpose is not to discuss such an isolated element to interpret hominid locomotion. We rather believe that a network of elements suggests that, as in humans walking on a soft support, Laetoli hominids flexed toes at ground contact, and extended them at toe-off. Extended or flexed digits are not merely a problem of shape, but above all a problem of how to propel body. Elftman and Manter [15] noticed that there is no metatarsal pressure in a chimpanzee walking bipedally

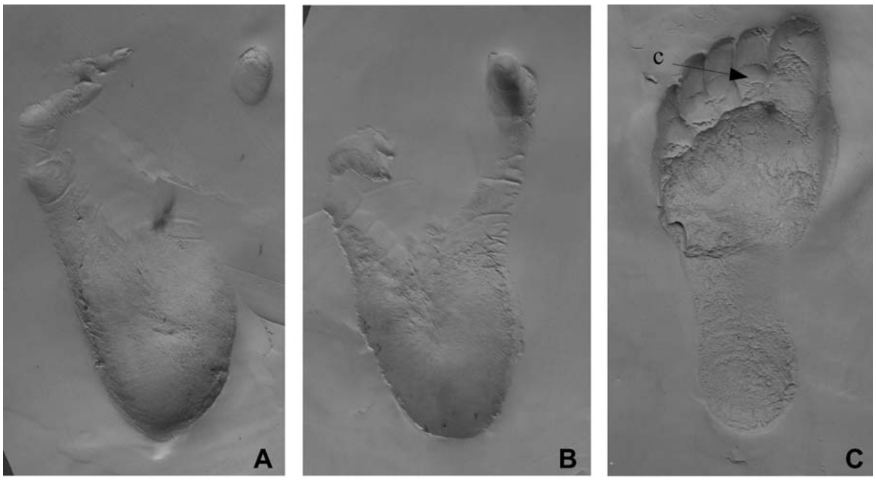

Fig. 4. Flexed or curled-underneath toes in chimpanzees and humans walking on soft subtract. (**A**) *Pan*: permanently flexed lateral toes in right foot (reversed photo); (**B**) *Pan*: permanently curled-underneath lateral toes in left foot. (**C**) *Homo*: flexed toes at ground contact, extended toes at toe-off; **c**: cupules corresponding to adherent surfaces of first phalanges with wet ground at toe-off (see text).

Fig. 4. Orteils fléchis ou repliés chez les chimpanzés et les humains marchant sur un sol mou. (**A**) *Pan* : orteils latéraux fléchis en permanence au pied droit (photo inversée) ; (**B**) *Pan* : orteils latéraux repliés en permanence au pied gauche ; (**C**) *Homo* : orteils fléchis au contact avec le sol, étendus au levé des orteils ; **c** : cupules correspondant aux surfaces d'adhérence des premières phalanges avec le sol humide au levé des orteils (voir texte).

because the metatarso-phalangeal joint in chimpanzees is so arranged that the foot cannot be flexed as a whole in this region. At foot-off, the chimpanzee cannot push on the ball and digits, but uses heel and midfoot (toes being passive) to propel itself. On the contrary, humans propel themselves by pushing on the hyperextended metatarso-phalangeal joint and toes. We believe that this was also the mode of propulsion in Laetoli, as demonstrated below with metatarsal centres of pressure.

Our results allow us to assert certain facts. Laetoli prints belong to a non-human species (*Australopithecus*) clearly discriminated from any prints of modern humans. Numerous elements indicate that the fossils possessed both human-like and ape-like traits in terms of morphology, footfall and body weight transfer. Here statistics and shape analyses suggest that the fossils were clearly closer to humans than to chimpanzees. This may be partly due to the fact that our chimpanzee walked on the lateral edge of the foot with flexed or curled-underneath digits, whereas in Laetoli, the foot was more internally turned and digits differently positioned. However, other elements prove that the Laetoli foot acted more like a human foot than that of a chimpanzee. Laetoli hominids had (1) a noticeable foot vault, (2) metatarsal supports (ball of the foot), and (3) human-like digit ground contact and toe-off. They walked bipedally, with feet completely flat on the ground, relatively human-like short stride lengths, similar feet orientation, and small feet gap. They probably walked also with low velocity, because deep heel prints suggest that they used their heels as brakes to avoid slipping. Although they preserved ape-like traits such as a foot roll-off at stance phase, they already possessed the seeds of human-like traits which are necessary to travel bipedally on the ground. Functional and structural traits already human-like in fossils (vault, ball of the foot) suggest that the australopithecines used to travel bipedally in long distances on the ground, even though they preserved anatomical ape-like traits on foot morphology.

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