

The Laetoli footprints and early hominin locomotor kinematics

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Abstract

A critical question in human evolution is whether the earliest bipeds walked with a bent-hip, bent-knee gait or on more extended hindlimbs. The differences between these gaits are not trivial, because the adoption of either has important implications for the evolution of bipedalism. In this study, we re-examined the Laetoli footprints to determine whether they can provide information on the locomotor posture of early hominins. Previous researchers have suggested that the stride lengths of Laetoli hominins fall within the range of modern human stride lengths and therefore, Laetoli hominins walked with modern-human-like kinematics. Using a dynamic-similarity analysis, we compared Laetoli hominin stride lengths with those of both modern humans and chimpanzees. Our results indicate that Laetoli hominins could have used either a bent-hip, bent-knee gait, similar to a chimpanzee, or an extended-hindlimb gait, similar to a human. In fact, our data suggest that the Laetoli hominins could have walked near their preferred speeds using either limb posture. This result contrasts with most previous studies, which suggest relatively slow walking speeds for these early bipeds. Despite the many attempts to discern limb-joint kinematics from Laetoli stride lengths, our study concludes that stride lengths alone do not resolve the debate over early hominin locomotor postures.

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Introduction

The adoption of bipedalism is considered a defining event in human evolution. Despite its importance, however, we still do not fully understand the locomotor biomechanics of early hominins, which limits our ability to determine why bipedalism evolved in the hominin lineage. Much debate has centered on whether early bipeds (and more specifically, australopiths) used flexed hindlimb joints, similar to chimpanzees walking bipedally, or extended hindlimb joints, similar to modern humans (Lovejoy, 1974; Stern and Susman, 1983; Latimer, 1991; Stern, 2000). The differences between these gaits are not trivial, because the adoption of either has important implications for how bipedalism evolved. For example, if early hominins walked with flexed hips and knees, any hypothesized

selection pressure must account for the higher energetic costs of this gait compared to the use of more extended limb joints (see Crompton et al., 1998; Stern, 1999; Carey and Crompton, 2005).

In this study, we use the Laetoli footprints to re-examine locomotor biomechanics in early hominins. Site G at Laetoli, Tanzania, contains two footprint trackways dated to approximately 3.5 Ma that are considered indisputably hominin (Leakey and Hay, 1979; White, 1980). The trails of a smaller individual (G1) and a larger individual (G2) run parallel, with several researchers suggesting that the footprints of a third individual (G3) are superimposed onto those of G2 (Robbins, 1987; Tuttle, 1987; Tuttle et al., 1990). Most researchers believe *Australopithecus afarensis* is responsible for the trails (White, 1980; Stern and Susman, 1983; White and Suwa, 1987; but see Tuttle et al., 1990; Harcourt-Smith, 2006), indicating that the footprints could provide insights into a taxon at the center of the debate over early hominin locomotor postures and gaits.

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Most previous investigations of the morphology and the spatial orientation of the footprints have concluded that the Laetoli hominins walked with kinematics similar to modern humans (Leakey and Hay, 1979; Day and Wickens, 1980; White, 1980; Charteris et al., 1981, 1982; Alexander, 1984; Tuttle, 1987; Tuttle et al., 1990; Musiba et al., 1997), but others have suggested that the Laetoli trackways are consistent with a bent-hip, bent-knee gait (Stern and Susman, 1983). Additionally, several researchers have estimated kinematic parameters of early hominin gait by comparing the Laetoli stride lengths with those of modern humans (see Charteris et al., 1981, 1982; Alexander, 1984; Tuttle, 1987; Reynolds, 1987; Tuttle et al., 1990). The majority of these stride-length analyses concluded that the Laetoli hominins must have used a gait similar to that of modern humans, since their stride lengths fit modern human models (Charteris et al., 1981, 1982; Alexander, 1984; Tuttle, 1987; Tuttle et al., 1990). However, these analyses suggested relatively slow walking velocities (0.56–0.75 m/s) that are more consistent with walking speeds well-below normal human preferences (Charteris et al., 1981, 1982; Alexander, 1984; Tuttle, 1985, 1987; Tuttle et al., 1990, 1991).

Recently, Sellers et al. (2005) presented a more sophisticated biomechanical model also suggesting that the Laetoli hominins walked with modern human kinematics. Using a forward-dynamics simulation, these authors showed that a model of A.L. 288-1 (“Lucy”), walking with an extended limb posture, had stride lengths that fit the trails at a slightly higher velocity than others have suggested (0.65–1.0 m/s). This innovative work demonstrates that a Lucy-sized hominin could have made the Laetoli tracks while walking with extended hindlimb joints.

Thus, the available evidence from previous work indicates that the Laetoli trackways are consistent with an extended-hindlimb bipedal gait, but few studies to date have investigated whether the Laetoli footprints could also fit a more flexed hindlimb posture. Such analyses are crucial in order to determine the confidence with which an extended hindlimb posture may be assigned to the Laetoli hominins. One obstacle to performing such an analysis is the difficulty in obtaining kinematic data for adult chimpanzees. Chimpanzees provide a useful living model for the flexed bipedal postures proposed of early hominins for several reasons. First, since a *Pan-Homo* clade is well supported by genetic evidence (Ruvolo, 1994; Satta et al., 2000), and since chimpanzees, bonobos, and gorillas share many morphological similarities, it is reasonable to assume that the last common ancestor of chimpanzees and humans was a chimpanzee-like ape (Washburn, 1967; Pilbeam, 1996; Richmond and Strait, 2000). Second, when walking bipedally, chimpanzees use a bent-hip, bent-knee posture, which may resemble the early hominin postures suggested by Stern and Susman (1983). However, the lack of relevant data for bipedal walking in adult chimpanzees has prevented a flexed-posture analysis of the Laetoli trackways.

In this study, we tested the hypothesis that Laetoli hominins could have comfortably walked with a chimpanzee-like flexed hindlimb posture. To test this hypothesis, we compared Laetoli

hominin stride lengths with those of both modern humans and adult chimpanzees over a range of bipedal walking speeds. Since individuals typically choose a narrow range of stride lengths for a given walking speed (Bertram and Ruina, 2001), we assessed the probability that the Laetoli hominins used a flexed or extended posture by comparing the stride lengths of the Laetoli trackways against chimpanzee and human kinematic data. If the hominin footprints at Laetoli are consistent with both flexed- and extended-limb gaits, then the kinematic data available from these trackways may be insufficient for distinguishing between postures. We also present revised estimates of Laetoli hominin walking velocities, based on a dynamic-similarity analysis, and for the first time, we estimate velocities for Laetoli hominins had they walked with a flexed-limb gait.

Methods

A sample of humans ($n = 5$; mean body mass = 64.7 ± 6.2 kg) and adult chimpanzees (*Pan troglodytes*; $n = 5$; mean body mass = 59.8 ± 18.1 kg) participated in this study. We performed a dynamic-similarity analysis of human and chimpanzee stride lengths by combining measurements of hip height with walking kinematics. We then applied this dynamic-similarity analysis to the Laetoli trackways. All procedures were approved by the Harvard University Human Subjects Committee and both the Harvard University and University of California at Davis Institutional Animal Care and Use Committees. All human subjects signed informed consent forms. None of the human subjects had a prior history of lower-limb injury.

Estimating hip height

We estimated hip heights of Laetoli hominins using the relationship between foot length and hip height in both humans and chimpanzees. In this way, we could use the prints themselves to estimate Laetoli hip heights. For each subject, hip height (distance from the greater trochanter to the floor) and foot length (maximum anteroposterior length of the foot) were measured. Human hip heights and human and chimpanzee foot lengths were collected using measuring tape. Chimpanzee hip heights were measured from high-speed video (Redlake, Inc., 125 frames/second) at midstance. Hip height measured in this way is appropriate for comparisons of Froude number, as it measures the effective length of the limb as a strut. However, it should be noted that this effective hindlimb length is generally shorter than the summed lengths of the limb segments, particularly in chimpanzees and other animals that use crouched postures.

Foot-length index was calculated as foot length divided by hip height (human mean [SD] = 0.30 [0.01]; chimpanzee mean [SD] = 0.45 [0.05]). Hip height was calculated for the Laetoli hominins (Table 1) using both the human and chimpanzee foot-length indices, with Laetoli foot lengths measured from the G1 and G2 footprints (from Tuttle [1987]: G1 = 180.4 ± 4.8 mm; G2 = 208.8 ± 11.6 mm). Estimated hip heights were

Table 1
Estimated Laetoli hominin Froude numbers and velocities

Trackway	Model		Hip height (m)	Froude number		Velocity (m/s)					
	Hip height	Kin.		Mean (SD)	10% shorter foot	Mean (SD)	10% shorter foot	Sellers et al. (2005)	Charteris et al. (1981)	Alexander (1984)	Tuttle (1987)
G1	Human	Human	0.60	0.16 (0.06)	0.25	0.98 (0.18)	1.15	0.70	0.56	0.64	0.72
G1	Human	Chimp	0.60	0.05 (0.02)	0.07	0.52 (0.09)	0.61				
G1	Chimp	Human	0.40	0.88 (0.35)	1.36	1.86 (0.34)	2.19				
G1	Chimp	Chimp	0.40	0.25 (0.10)	0.39	0.99 (0.18)	1.18				
G2	Human	Human	0.69	0.11 (0.02)	0.17	0.86 (0.08)	1.02	1.00	0.72	0.75	0.86
G2	Human	Chimp	0.69	0.03 (0.01)	0.05	0.46 (0.04)	0.55				
G2	Chimp	Human	0.46	0.59 (0.12)	0.92	1.64 (0.16)	1.94				
G2	Chimp	Chimp	0.46	0.17 (0.03)	0.26	0.88 (0.08)	1.04				

similar to those of previous analyses of *A. afarensis* (mean = 54 cm, range = 46–70cm; Table 1). Because foot impressions in the soft, wet Laetoli substrate could overestimate foot length (due to slippage), we also calculated hip heights for Laetoli hominins using foot lengths that are 10% shorter than measured footprints. Although this value is necessarily arbitrary, it will demonstrate the impact of foot dimensions on estimated velocities.

Estimating velocity—dynamic similarity

Subjects walked bipedally on motor-driven treadmills (for humans: Vision Fitness T9250, Lake Mills, WI; for chimpanzees: Smooth Fitness 9.15, Sparks, NV) at a variety of speeds. Human subjects wore footswitches (Motion Analysis Inc.) to indicate touchdowns. Touchdowns for chimpanzees were found using high-speed video (Redlake, Inc., 125 frames/second). Stride length was calculated as the product of stride duration (time between successive touchdowns of the same foot) and treadmill velocity. Although treadmills clearly have different substrate characteristics than those found at Laetoli, several studies have shown that substrate compliance does not impact the relationship between walking velocity and stride length (Alexander, 1989; Lejeune et al., 1998; Kerdok et al., 2002).

We used the principle of dynamic similarity (Alexander and Jayes, 1983) to estimate walking velocity in the Laetoli hominins and to account for differences in hindlimb length between the extant and extinct samples. At a given dimensionless velocity, animals that are geometrically similar generally walk with equivalent dimensionless kinematic parameters, including stride length (Alexander and Jayes, 1983). Using dynamic similarity to estimate Laetoli walking velocities assumes that early hominins had geometrically similar limb lengths compared to either modern humans or to chimpanzees. There is reason to believe the Laetoli hominins did not have geometrically similar limb lengths, since *A. afarensis* had relatively shorter hindlimbs than modern humans and relatively longer hindlimbs than chimpanzees (see Jungers, 1982). Therefore, velocity estimations based on human and chimpanzee models will serve as boundaries for the actual Laetoli walking velocities, with chimpanzee-based estimates providing an upper bound and human-based estimates providing a lower bound.

For each human and chimpanzee subject, we calculated a dimensionless velocity and dimensionless stride length at a variety of treadmill velocities. Velocity (v) was made dimensionless using the Froude number, F , where $F = v^2/gh$, g is gravity, and h is hip height. Stride length was made dimensionless by dividing stride length by hip height. Dimensionless stride lengths were regressed on Froude numbers in log space and least-squares regressions were calculated for the human and chimpanzee data sets, respectively.

For the Laetoli hominins, dimensionless stride length was estimated by dividing mean stride length for each trackway, taken from data in Tuttle (1987), by estimated hip height (Table 1). Note that, here, stride length is defined as the distance between two ipsilateral heel-strikes (e.g., right footprint to subsequent right footprint). This formulation differs from that in other studies (Charteris et al., 1981, 1982; Alexander, 1984), in which step lengths (e.g., right footprint to left footprint) were doubled to calculate stride length, but is more comparable to most treatments of stride length and locomotor kinematics (e.g., Alexander and Jayes, 1983). Dimensionless stride lengths were then used to calculate Froude numbers and walking velocities ($v = [Fgh]$) for the Laetoli hominins using the chimpanzee and human regressions. The use of two hip-height estimates and two regression equations to calculate dimensionless stride lengths and speeds resulted in four possible walking velocities for each Laetoli hominin (Table 1): (1) human hip-height estimates combined with human stride-length regression model; (2) chimpanzee hip-height estimates combined with human stride-length regression model; (3) chimpanzee hip-height estimates combined with chimpanzee stride-length regression model; and (4) human hip-height estimates combined with chimpanzee stride-length regression model. Finally, we calculated error bounds for these estimates using the standard deviation for mean stride-length measurements in Tuttle (1987).

Results

Walking velocities for G1 and G2 estimated using human-like hip heights and the human stride-length regression model (0.98 m/s and 0.86 m/s for G1 and G2, respectively; Table 1) are higher than most previous studies have found and are

more similar to each other than those calculated by previous researchers (Table 1). Our predicted velocities correspond to Froude numbers of 0.16 and 0.11 for G1 and G2, respectively. These values are within the range of those used by other mammals, including modern humans whose preferred walking velocities fall between 0.8 m/s and 1.7 m/s (Bornstein and Bornstein, 1976). When velocities are estimated using human-like hip heights and chimpanzee-like kinematics, the estimated velocities for the Laetoli hominins are much slower (0.52 and 0.46 m/s; Table 1) and Froude numbers generally fall towards the lower range of values used by mammals (0.05 and 0.03; the lowest Froude numbers used by mammals in Alexander and Jayes [1983] were just below 0.1).

If the Laetoli hominins had relative hip heights more similar to those of chimpanzees, the results change dramatically. Velocities based on the modern human stride-length regression model are higher (1.84 and 1.64 m/s for G1 and G2, respectively; Table 1). In fact, Froude numbers for these estimations (0.88 and 0.59) indicate running velocities, as the walk-run transition typically occurs at a Froude number of 0.5 (Alexander and Jayes, 1983). Since there is no indication of running gaits from the footprints themselves, estimations based on chimpanzee kinematics are more realistic, given a chimpanzee-like hip height (0.99 and 0.88 m/s for G1 and G2, respectively; Table 1). Froude numbers for these estimations (0.25 and 0.17 for G1 and G2, respectively) are similar to those used by most mammals walking at preferred speeds ($F = 0.25$).

It is important to note that the chimpanzee-like hip heights for the Laetoli hominins are slightly shorter than they would be if calculated using an extended posture. If early hominins had relatively shorter hindlimbs than modern humans, but walked with extended limb postures (leading to a foot-length-to-hip-height ratio of 0.42), their Froude numbers would have been 0.66 ($v = 1.66$ m/s) and 0.45 ($v = 1.47$ m/s) for G1 and G2, respectively. Although these values are slower than those estimated using chimpanzee flexed-limb hip heights, the overall results do not change. The Laetoli individuals would have either been walking very near the walk-run transition (e.g., $F = 0.50$) or they would have been running (e.g., $F > 0.50$).

In all cases, if actual hominin foot lengths were 10% smaller than the footprint lengths, estimated walking velocities increase (Table 1). This increase in velocity places the human hip height, human kinematics scenario closer to preferred walking velocities, but does not otherwise fundamentally alter the results. The data do suggest, however, that the velocity estimates are subject to preservation errors and must therefore be interpreted with caution.

Discussion

The results from this study provide revised estimates of Laetoli hominin walking velocities and offer a new basis for interpreting Laetoli hominin kinematics. Previous estimations neglected the possibility that the Laetoli hominins walked with

flexed-hip, flexed-knee kinematics (Charteris et al., 1981, 1982; Alexander, 1984; Tuttle, 1987; Tuttle et al., 1990; Sellers et al., 2005). Several authors have concluded that the Laetoli hominins likely used humanlike kinematics because their estimates fit human models (Charteris et al., 1981, 1982; Alexander, 1984; Tuttle, 1987; Tuttle et al., 1990; Sellers et al., 2005). Our results suggest that the Laetoli footprints can fit either a human-like or a chimpanzee-like model of locomotor kinematics.

As noted above, it is likely that the Laetoli hominins were not geometrically similar to either modern humans or to chimpanzees, and therefore our model predictions, which assume geometric similarity, must be viewed as upper and lower boundaries for actual Laetoli hominin Froude numbers and velocities. However, insofar as Laetoli hominin relative hindlimb lengths fall somewhere between those of modern humans and chimpanzees (Jungers, 1982), we can be reasonably certain that their Froude numbers would have fallen in between our estimates based on the human and chimpanzee models. A second note of caution is necessary when interpreting the G2 prints, since they likely represent those of two individuals. Therefore, foot lengths and stride lengths for the G2 trackways are not as accurate as are those of G1.

One final concern in using these methods to estimate Laetoli hominin kinematics is that treadmill kinematics may not accurately predict the kinematics of walking on other substrates (such as the soft, wet Laetoli substrate). Several authors have, however, found that changes in substrate characteristics do not significantly alter the relationship between stride length and velocity (Alexander, 1989; Lejeune et al., 1998; Kerdok et al., 2002). This relationship held during human locomotion on sand (Alexander, 1989; Lejeune et al., 1998) and on an experimentally altered treadmill that simulated substrates of varying stiffness (Kerdok et al., 2002). Therefore, although we cannot be certain that the Laetoli hominins did not alter their kinematics on the wet ashfall, estimates of their walking velocities based on treadmill walking are appropriate. Future research should address the possibility that obstacles or substrate temperature could induce a different relationship between stride length and walking velocity, which could alter our estimation of Laetoli hominin walking velocities.

Given the cautions associated with the dynamic-similarity approach, and the lack of fossil postcrania from Laetoli, it is best to consider the velocity estimations as boundaries for the Laetoli hominins. Because mixed-taxon models (e.g., human hip height, chimpanzee kinematics) predict unreasonable velocities, the human hip height, human kinematics model represents the lower end of the predicted velocity range and the chimpanzee hip height, chimpanzee kinematics model represents the upper end of the velocity range. Froude numbers for G1 were likely between 0.16 and 0.25, and Froude numbers for G2 were likely between 0.11 and 0.17. Walking velocities calculated from the boundary Froude numbers are quite similar (0.98 and 0.99 for G1; 0.86 and 0.88 for G2), because hip heights differ greatly between the two boundary conditions. Thus, there is no reason to conclude that Laetoli hominin walking velocities must have been slow, since

scenarios exist that place the footprint makers at their preferred velocities (i.e., $F = \sim 0.25$).

Based on comparisons of the chimpanzee and human models, the conclusions reached by previous researchers regarding the Laetoli hominins are incomplete. That is, previous walking models correctly predict that if early hominins walked with modern-human-like kinematics, they could have easily made the footprint trails, but it is equally plausible that an early hominin walking with flexed hips and knees could have made the same trails walking at a normal pace. While the fit of human-like kinematics indicates an essentially modern human gait for these early hominins, as suggested by some (Lovejoy, 1974; Latimer, 1991), the fit of chimpanzee-like kinematics is consistent with anatomical evidence suggesting a bent-hip, bent-knee gait in australopiths (Stern and Susman, 1983; Stern, 2000). The speed and kinematics indicated by the trackway are insufficient for determining the posture and gait of the Laetoli hominins.

These results do, however, generate testable predictions for future studies examining early hominin kinematics at Laetoli. First, new discoveries of Laetoli hominin postcrania will resolve whether these individuals had foot-length-to-hip-height ratios more similar to chimpanzees or humans. Second, a more detailed understanding of how footprint morphology is generated will help determine whether high-speed gaits were used at Laetoli. The stride length models presented here suggest that if Laetoli hominins had foot-length-to-hip-height

ratios more similar to chimpanzees, and that high-speed gaits were not used at Laetoli, then it is more likely that these hominins walked with some degree of limb flexion. On the other hand, slightly longer hindlimbs or evidence of higher-speed gaits would suggest a more humanlike kinematic pattern.

In addition to the implications of our results for understanding early hominin kinematics, this study provides some new data on Laetoli hominin behavior. Previous studies predicted speeds that differ between the two trails by 15% to 30% (see Table 1), which could imply that the Laetoli hominins were not walking together. Following our methods, predicted speeds for G1 and G2 are more similar to each other, differing by 11% for all models (see Table 1). Given the error involved in these calculations (see Fig. 1), these results suggest that the individuals who made the footprint trails could have walked together across the ashfall.

Although the footprint trails at Laetoli offer a unique record of early hominin kinematics, no study to date has been able to convincingly detail Laetoli hominin biomechanics. Based on the models described above, early hominins could have plausibly created the Laetoli footprint trails using either relatively extended knees and hips or relatively flexed knees and hips. The Laetoli footprints continue to offer a tantalizing glimpse into early hominin bipedalism, but further insights into early hominin biomechanics must rely on a combination of variables in addition to stride length.

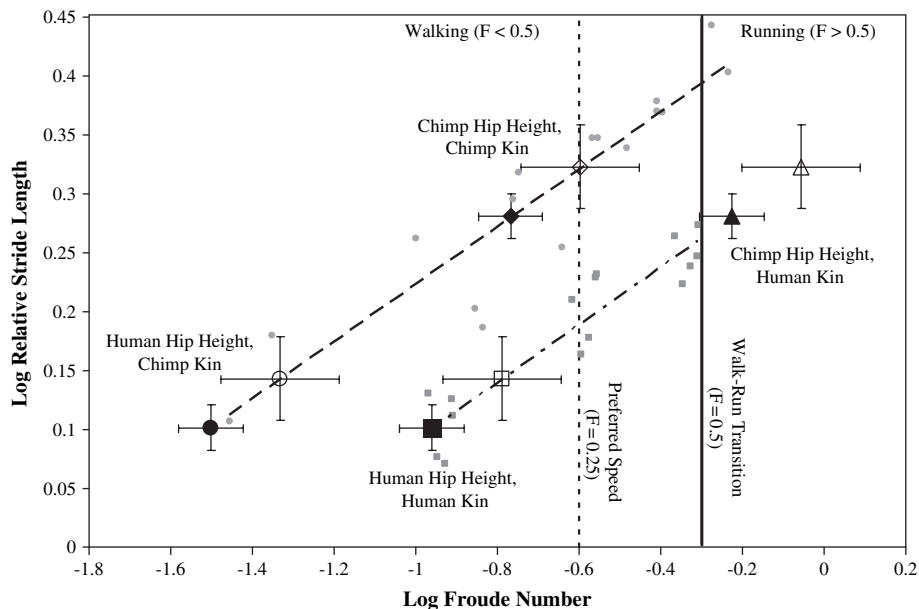


Fig. 1. Relationship between dimensionless stride length and Froude number in humans, chimpanzees, and Laetoli hominins. The dashed line is a least-squares regression line for chimpanzees (slope [95% confidence interval] = 0.24 [0.06]; intercept [95% CI] = 0.46 [0.04]; $r = 0.92$; $p < 0.001$). The solid line is a least-squares regression line for humans (slope [95% CI] = 0.24 [0.06]; intercept [95% CI] = 0.33 [0.04]; $r = 0.93$; $p < 0.001$). Gray circles are chimpanzees; gray squares are modern humans; black square and open square are G1 and G2, respectively, with human hip heights and human kinematics; black circle and open circle are G1 and G2, respectively, with human hip heights and chimpanzee kinematics; black triangle and open triangle are G1 and G2, respectively, with chimpanzee hip heights and human kinematics; black diamond and open diamond are G1 and G2, respectively, with chimpanzee hip heights and chimpanzee kinematics. Error bars are the lowest and highest values for each variable calculated using the standard deviation for measured stride length from Tuttle (1987). The dashed vertical line indicates preferred walking velocity ($F = 0.25$) and the solid vertical line indicates walk-run transition velocity ($F = 0.5$).

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References

- Alexander, R.M., 1984. Stride lengths and speed for adults, children, and fossil hominids. *Am. J. Phys. Anthropol.* 63, 23–27.
- Alexander, R.M., 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. Columbia University Press, New York.
- Alexander, R.M., Jayes, A.S., 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool. Lond.* 201, 135–152.
- Bertram, J., Ruina, A., 2001. Multiple walking speed-frequency relations are predicted by constrained optimization. *J. Theoret. Biol.* 209, 445–453.
- Bornstein, M.N., Bornstein, H.G., 1976. The pace of life. *Nature* 259, 557–558.
- Carey, T., Crompton, R.H., 2005. The metabolic cost of 'bent-hip, bent-knee' walking in humans. *J. Hum. Evol.* 48, 25–44.
- Charteris, J., Wall, J.C., Nottrodt, J.W., 1981. Functional reconstruction of gait from the Pliocene hominid footprints at Laetoli, northern Tanzania. *Nature* 290, 496–498.
- Charteris, J., Wall, J.C., Nottrodt, J.W., 1982. Pliocene hominid gait: new interpretations based on available footprint data from Laetoli. *Am. J. Phys. Anthropol.* 58, 133–144.
- Crompton, R.H., Li, Y., Wang, W.J., Gunther, M., Savage, R., 1998. The mechanical effectiveness of erect and "bent-hip, bent-knee" bipedal walking in *Australopithecus afarensis*. *J. Hum. Evol.* 35, 55–74.
- Day, M.H., Wickens, E.H., 1980. Laetoli Pliocene hominid footprints and bipedalism. *Nature* 286, 385–387.
- Harcourt-Smith, W.E., 2006. Did *Australopithecus afarensis* make the Laetoli footprint trail? New insights into an old problem. *Am. J. Phys. Anthropol.* 40 (Suppl.), 112.
- Jungers, W.L., 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297, 676–678.
- Kerdok, A.E., Biewener, A.A., McMahon, T.A., Weyand, P.G., Herr, H.M., 2002. Energetics and mechanics of human running on surfaces of different stiffness. *J. Appl. Physiol.* 92, 469–478.
- Latimer, B., 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les Hominides*. CRNS Editions, Paris, pp. 169–176.
- Leakey, M.D., Hay, R.L., 1979. Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania. *Nature* 278, 317–323.
- Lejeune, T.M., Willems, P.A., Heglund, N.C., 1998. Mechanics and energetics of human locomotion on sand. *J. Exp. Biol.* 201, 2071–2080.
- Lovejoy, C., 1974. The gait of australopithecines. *Yearb. Phys. Anthropol.* 17, 147–161.
- Musiba, C.M., Tuttle, R.H., Hallgrímsson, B., Webb, D.M., 1997. Swift and sure-footed on the savanna: a study of Hadzabe gaits and feet in northern Tanzania. *Am. J. Hum. Biol.* 9, 303–321.
- Pilbeam, D.R., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. *Mol. Phylogenet. Evol.* 5, 155–168.
- Reynolds, T.R., 1987. Stride length and its determinants in humans, early hominids, primates, and mammals. *Am. J. Phys. Anthropol.* 72, 101–115.
- Richmond, B.G., Strait, D.S., 2000. Evidence that humans evolved from a knuckle-walking ancestor. *Nature* 404, 382–385.
- Robbins, L.M., 1987. Hominid footprints from site G. In: Leakey, M.D., Harris, J.M. (Eds.), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford, pp. 497–502.
- Ruvolo, M., 1994. Molecular evolutionary processes and conflicting gene trees: the hominoid case. *Am. J. Phys. Anthropol.* 94, 89–114.
- Satta, Y., Klein, J., Takahata, N., 2000. DNA archives and our nearest relative: the trichotomy revisited. *Mol. Phylogenet. Evol.* 14, 259–275.
- Sellers, W., Cain, G., Wang, W., Crompton, R.H., 2005. Stride length, speed and energy costs in walking of *Australopithecus afarensis*: using evolutionary robotics to predict locomotion of early human ancestors. *J. Roy. Soc. Interface* 2, 431–441.
- Stern, J.T., 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. *Evol. Anthropol.* 9, 113–133.
- Stern, J.T., 1999. The cost of bent-knee, bent-hip gait. A reply to Crompton, et al. *J. Hum. Evol.* 36, 567–570.
- Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279–317.
- Tuttle, R.H., 1985. Ape footprints and Laetoli impressions: a response to SUNY claims. In: Tobias, P.V. (Ed.), *Hominid Evolution: Past, Present and Future*. Liss, New York, pp. 129–133.
- Tuttle, R.H., 1987. Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1, G-2/3, and A. In: Leakey, M.D., Harris, J.M. (Eds.), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford, pp. 503–520.
- Tuttle, R.H., Webb, D., Weidl, E., Baksh, M., 1990. Further progress on the Laetoli trails. *J. Archaeol. Sci.* 17, 347–362.
- Tuttle, R.H., Webb, D.M., Tuttle, N.I., 1991. Laetoli footprint trails and the evolution of hominid bipedalism. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les Hominides*. CRNS Editions, Paris, pp. 187–198.
- Washburn, S.L., 1967. Behavior and the origin of man. *Proc. R. Anthropol. Inst. Gr. Br. Ire.* 3, 21–27.
- White, T.D., 1980. Evolutionary implications of Pliocene hominid footprints. *Science* 208, 175–176.
- White, T.D., Suwa, G., 1987. Hominid footprints at Laetoli: Facts and interpretations. *Am. J. Phys. Anthropol.* 72, 485–514.