PEDAL MECHANICS AND BIPEDALISM IN EARLY HOMINIDS

by John H. LANGDON

Department of Biology, University of Indianapolis, USA

Jan BRUCKNER

Physical Therapy Program, Indiana University School of Medicine, Indianapolis, USA

H. Harlyn BAKER

Artificial Intelligence Center, SRI International, Menlo Park, California, USA

RÉSUMÉ. – La mécanique du pied et la bipédie chez les premiers Hominidés.

Aucune théorie sur l'origine de la bipédie n'est actuellement universellement reconnue. Les scénarios les plus populaires font référence aux conséquences culturelles observées chez l'homme moderne pour expliquer les changements dans les populations non-humaines. Les hypothèses culturelles sur l'évolution des hominidés qui prédatent toute preuve d'une culture complexe sont au mieux spéculatives. Un autre groupe d'hypothèses, que nous favorisons, considère la bipédie comme un moyen d'accroître l'efficacité du comportement de position dans les arbres ou au sol.

Les études morphologiques actuelles peuvent nous aider à comprendre ce phénomène évolutif en le localisant dans le temps et en établissant les grandes lignes de ses modalités anatomique, comportementale et écologique.

Le pied humain présente une capacité unique à faire alterner deux modes fonctionnels : une configuration laxiste pour le support statique de poids et l'absorption des chocs et un levier très stable pour la propulsion. Les deux sont utilisés au cours des différentes phases de la marche normale. Le mécanisme de conversion qui permet le passage d'un mode à l'autre est rendu possible grâce en partie au changement de l'alignement des axes de l'articulation tarsienne sous-talaire et transverse dans la supination et la pronation. L'acquisition d'un pied rigide et de son arc longitudinal est une adaptation cruciale pour une bipédie efficace.

Nous avons étudié des os actuels et des moulages d'Hominidés plio-pléistocènes. Les os individuels, les moulages et les pieds articulés ont été scannographiés et photographiés pour reconstituer et manipuler les articulations. Dans notre travail qui est toujours en cours, nous calculerons les axes en superposant des courbes sur les surfaces articulaires.

Les premiers résultats indiquent que les articulations talonaviculaire et calcanéocuboïde des fossiles ressemblent beaucoup à celles de l'homme et s'éloignent du chimpanzé. Nous suggérons que le pied des hominidés anciens était capable morphologiquement de transmettre une redistribution de pression et de maintenir l'équilibre, caractères que nous associons à la bipédie moderne, et que très probablement il possédait un mécanisme de conversion et un arc longitudinal médial fonctionnel.

Cette reconstruction du pied des Hominidés anciens conforte les données publiées auparavant sur les adaptations à la bipédie de ces hominidés. Le comportement bipède terrestre des Hominidés plio-pléistocènes est établi sans aucun doute par les empreintes de pas de Laetoli, datées de 3.6 M.a., et pratiquement chaque adaptation squelettique à la bipédie identifiée chez l'homme moderne est présente à un certain degré chez les Australopithèques et différencie ces derniers des autres hominoïdes. En revanche, les preuves d'une évolution culturelle significative apparaissent plus tard.

Ces conclusions s'ajoutent à d'autres résultats qui montrent que la transition vers la bipédie, avec ses adaptations morphologiques essentielles, s'est faite très tôt, peut-être avant qu'aucun autre trait distinctif humain, ne soit présent. Ces résultats supportent donc l'hypothèse que la bipédie terrestre est une adaptation primaire et originale de la lignée humaine. D'autres caractères comportementaux humains ont évolué plus tard et ne peuvent pas être considérés comme causes de la bipédie.

ABSTRACT

No hypothesis accounting for the origin of bipedalism has gained universal acceptance at the present time. The most popular hypotheses have used cultural consequences observed in modern humans to explain changes in a non-human population. Cultural assumptions about hominids who predate any evidence for complex culture are speculative at best. Another set of hypotheses, which we favor, views bipedalism as a means of increasing efficiency of arboreal or terrestrial positional behavior.

Current morphological studies can help us to understand this evolutionary event by locating it in time and by mapping out its anatomical, behavioral, and ecological pathways. To this end, we investigate the tarsal mechanics of the Plio-Pleistocene hominids.

The human foot displays a unique ability of alternate between two functional modes – a loose-packed configuration for static weight-bearing and shock-absorption and a close-packed rigid lever for propulsion. Both are utilized in different phases of normal gait. The conversion mechanism that permits the shift from one mode to the other is made possible in part by the changing alignment of the subtalar and transverse tarsal joint axes in supination and pronation. The creation of a rigid foot and its longitudinal arch is a critical adaptation for efficient bipedalism.

We examined skeletal material and casts of Plio-Pleistocene hominid fossils. Individual bones, casts, and articulated feet were scanned with computerized tomography and imaged for joint reconstruction and manipulation. In our continuing work, axes will be computed by fitting curves to the articular surfaces.

Preliminary results indicate that the talonavicular and calcaneocuboid articulations in the fossils closely resemble those of humans and differ from those of the chimpanzee. We infer that the early hominid foot was morphologically capable of providing the redistribution of pressure and the maintenance of balance that we associate with modern bipedalism, and most likely possessed a conversion mechanism and a functional medial longitudinal arch.

This reconstruction of the early hominid foot supports much previously published evidence of extensive adaptations to bipedalism among the earliest hominids. Terrestrial bipedal behavior of the Plio-Pleistocene hominids is established beyond doubt by the Laetoli footprints, dated at 3.6 M.a., and nearly every skeletal adaptation to bipedalism identified in modern humans is present to some degree in the australopithecines to differentiate them from other hominoids. In contrast, all evidence for significant cultural advances occurs later.

These inferences add to the accumulating evidence that the transition to bipedalism, with extensive morphological adaptations, occurred very early, perhaps before any other of the distinctive human traits. We interpret this to support the hypothesis that terrestrial bipedalism was the primary and original adaptation of the hominid lineage. Other human behavioral characters evolved later and were not causal to bipedalism.

INTRODUCTION

Current models to explain the evolution of human bipedalism focus on either culture or functional anatomy. Cultural hypotheses explain bipedalism as an adaptation for culture and social interaction. Anatomical hypotheses view bipedalism as a means to increase efficiency of arboreal and/or terrestrial positional behavior. Both sets of hypotheses have a long history in paleoanthropology and, by their natures, are unlikely to be easily proved or disproved.

Cultural hypotheses since Darwin have centered on one or more aspects of behavior considered unique to human society and, from these, constructed networks of causal interrelationships leading to a modern picture of culture. Past themes of such hypotheses have addressed tools, weapons, diet, and ecological niche. Of current interest is a focus on the family structure and its economy (e.g. Lancaster, 1978 ; Lovejoy, 1981 ; Tanner, 1981).

Anatomical models have shown more kinship with biological sciences than with cultural anthropology. Past debate has centered on the appropriate selection of a living ape as a model for the proto-hominid ancestor. In current arguments, the adaptations to arboreal climbing, including orthograde posture, increased reliance on hind limbs as supports, and reduced efficiency of terrestrial locomotion, are presumed to have made the commitment to bipedalism less traumatic (e.g. Fleagle *et al.*, 1981 ; Langdon, 1985 ; Tuttle, 1981).

Gould (1989) used the term "historical contingency" to express the idea that the distinguishing characteristics of a given species are the consequences of its unique history, and that such characteristics will further determine how that species will respond in an evolutionary sense to new challenges. An explanation of cause for an evolutionary event, such as the achievement of human bipedalism, lies in the past and present of the species, including the selective forces acting upon it, at the time of the event. Our reconstructions are necessarily retrospective, dominated by a knowledge of the evolutionary outcome. Gould therefore concludes that our models tend to be "progressive" and to have a deceptive appearance of "predictive" capability.

We argue that the functional anatomical models which attempt to reconstruct the proto-hominid ancestor are more likely to discover the historical contingencies which favored the evolution of bipedalism and may be less prone to the bias of cultural hindsight. Crucial to distinguishing between these two sets of hypotheses is the establishment of a relative chronology of anatomical, ecological, and behavioral changes. Ultimately it will be necessary to construct a map of the behavioral and functional transformation to bipedalism, although it is premature to attempt such a map in detail at this time.

In outlining these issues, we present an additional avenue of investigation as to whether the foot of the earliest known hominids had already acquired the mechanics crucial to human bipedalism. We believe that such studies can help to place temporal limits for the transition to bipedalism.

The human foot has the unique ability to alternate between two functional modes – a loose-packed configuration for static weight-bearing and shock-absorption and a close-packed rigid lever for propulsion. Both are utilized in different phases of normal gait. The conversion mechanism that permits the shift from one mode to the other is made possible in part by the arrangement of the subtalar and transverse tarsal joint axes and their ability to define supination and pronation.

At the beginning of the stance phase of human gait, the foot is in its loose-packed configuration. At that time, the subtalar joint is in pronation ; ligaments are more lax ; and the longitudinal arches of the foot are low. The axes of the talonavicular and calcaneocuboid joints permit a small degree of simultaneous movement. The foot has an increased ability to conform to the substrate and to absorb the shock of heel strike.

In the later phases of stance phase, especially following heel-off, the tarsals assume a close-packed configuration. The talus supinates within the foot. As it does so, the ligaments tighten and lock the joint. The talonavicular joint forms the center of a rigid chain of bones in which the medial longitudinal arch is increased in height. The two parts of the transverse tarsal joints are now stacked one above the other and prevent midfoot flexion in a sagittal plane (Close *et al.*, 1967). Furthermore, their axes have shifted further out of alignment and prevent simultaneous movement (Elftman, 1960). Thus at least three factors contribute to inhibiting midfoot motion : ligament tension, stacking of the joints, and oblique alignment of the axes (fig. 1).

The tarsus (literally "plate") has frequently been likened to a twisted sheet of bones, with the anterior part of the foot horizontal and the posterior part more or less vertical. A greater degree of supination corresponds to an increase in the "twist" and increased resistance to midfoot flexion.
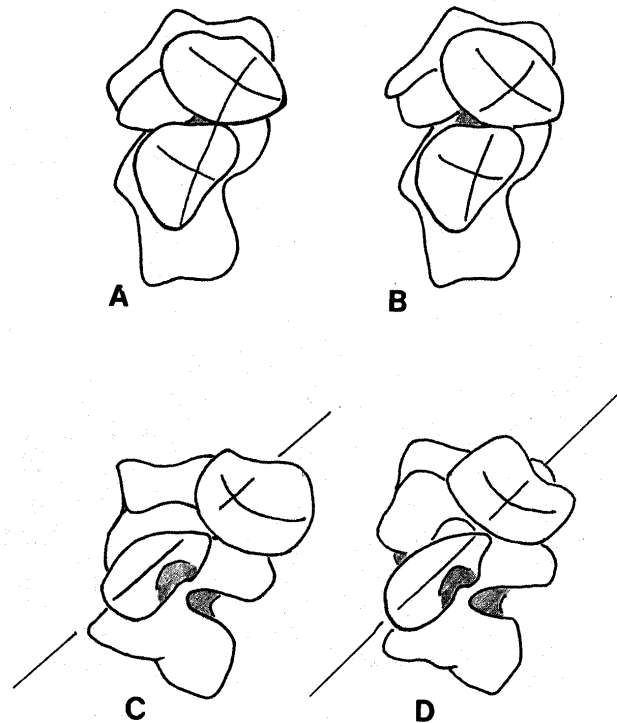

Fig. 1. – The conversion mechanism of idealized human and chimpanzee feet, as seen in anterior view of the talus and calcaneus. The approximate axes of curvature are indicated, showing the paths available for normal joint motion. In pronation (A) the axes of the human calcaneus and talus are aligned, and therefore permit some motion. Supination (B) disrupts the alignment of the two midfoot articulations and inhibits flexion. Comparable views of the chimpanzee foot in pronation (C) and supination (D) show that the alignment is maintained and midfoot dorsiflexion is possible about the indicated axis throughout the range of subtalar motion.

The orientations of the subtalar and transverse tarsal axes in relation to the rest of the foot, particularly in the rigid configuration, allow the joints to participate in several important aspects of bipedal stance and locomotion :

Pressure distribution. In both static and dynamic postures, the axis of the subtalar joint allows for a balanced distribution of weight among the five metatarsal heads (Jones, 1945). Regular adjustment of the pressure in stance reduces fatigue on any one part of the foot.

Conformation. When the ground or other supporting surface is not level or is not regular, the ankle and peritalar joints permit the sole of the foot to approximate the ground. This again helps to distribute pressure and maintain footing.

Balance. Active changes in pressure within the sole acting through a closed kinetic chain provide and ultimate fine-tuning of the balance of body mass on the supporting limb.

Resiliency. The tense soft tissues reinforcing the longitudinal arch can absorb and return kinetic energy. This reduces the shock on the bones and conserves energy simultaneously.

Propulsion. A rigid foot at the appropriate phase of gait provides an extended lever arm by which the posterior crural muscles can propel the body, thus increasing stride length.

Redirection of forces. Dynamic shifts of the subtalar joint during the propulsive phase of gait will result in a redirection of locomotor thrust from the metatarsus. Within a normal stride, eccentric contraction of the peroneal muscles acts to direct weight across the midline in preparation for acceptance by the opposite limb. Changes in the balance of the muscles can produce changes in the direction of travel.

The corresponding anatomy of a chimpanzee foot, as a model for the proto-hominid ancestor, differs from that of the human foot in critical ways. Ligaments and tendons allow greater accessory movement in the intrinsic joints. Articular facets permit greater joint excursion at the ankle and subtalar joints, and plantar and dorsiflexion occur at the transverse tarsal joint.

Within an ape foot, certain of the mechanical attributes of the human peritalar joints are absent (Elftman and Manter, 1935). In particular, there is no mechanism to convert to a rigid functional mode. A relative looseness of the intrinsic joints permits ready conformation of the foot to the substrate, whether ground or a tree limb.

The plate of the tarsus remains untwisted in a stance on a flat substrate. Weight is supported primarily in the proximal foot. The propulsive lever is shorter ; thus the *m. triceps surae* acts with greater mechanical advantage but yield a shorter stride. Both redirection of propulsive forces and balance center only in the posterior foot and thus are reduced in effectiveness. A bipedal chimp must rely on the less efficient strategy of a wide-based gait with greater expenditures of energy of the body mass.

Thus the conversion mechanism is a critical development in human bipedalism. We ask whether the early hominids had the conversion mechanism and whether they walked with a functionally rigid medial longitudinal arch.

MATERIALS AND METHODS

Skeletal material and casts of fossils for this study were made available to us from the Hammond-Todd Collection at the Cleveland Museum of Natural History. These included foot bones of *Homo sapiens* and *Pan troglodytes*. All recent specimens were adults, but they were selected at random with respect to size and sex. We examined casts of Plio-Pleistocene fossils, including AL 288-1 (Lucy) talus ; TNM 1517 partial talus ; KNM ER 1464 talus ; AL 333-8, AL 333-37, and 333-54 calcanei ; OH 8 articulated foot ; and Omo 33.74.895 calcaneus.

The casts and one chimpanzee talus and calcaneus were analyzed with an Elscint computerized tomography scanner. Slices 1.3 mm thick were scanned at intervals of 1.5 mm. Reconstituted computer images posses a pixel size corresponding to 0.55 mm on the original bones. In addition, a foot of one of us (JB) and a previously frozen foot of a subadult chimpanzee were scanned in three position (supinated, neutral and pronated). The chimpanzee specimen was also obtained by loan of the Cleveland Museum.

Data from the scanner were processed and analyzed by software for three-dimensional reconstruction and manipulation (figs. 2 and 3). This program identifies the surfaces of individual anatomical elements by recognizing changes in density in the original scan. One can then use the computer to manipulate these images independently, distinguish certain elements, make measurements, and simulate movements among them (Baker, 1988).

The position of the talus was standardized by passing a horizontal plane through the most superior points of the head and the two trochlear crests (fig. 2). The position of the calcaneus can be standardized by alignment of the facet for *m.triceps surae* with a coronal plane. For comparative purposes, the *sustentaculum tali* will be considered horizontal in posterior view.

The orientation of the joint axis for the subtalar articulation was then computed by curve-fitting. The anterior face of the posterior subtalar facet was approximated as a plane parallel to the axis. A series of parallel sections through the sustentacular facet perpendicular to the defined plane were fit to ellipses. The axis was calculated as a least squares fit of the centers of these ellipses (fig. 4). This procedure has produced a preliminary axis for the AL 288-1 talus (fig. 5) and offers the possibility of making direct quantitative comparisons with living species and with other fossils.

The axes generated from individual bones can be confirmed by checking them against axes generated by motion in intact or living individuals (work in progress). Such axes can be readily calculated to represent the net motion from one position to another.

A further estimation of relative position of the axis of the talonavicular joint was made by a conventional measurement

Fig. 2. – Computer generated reconstruction of AL 288-1 talus in stereo perspective. The talus has been oriented to a horizontal plane as defined in the text. The arrow represents a preliminary estimation of the subtalar axis.

Fig. 3. – Wire-frame reconstruction of the AL 288-1 talus in inferior view.

in anterior view of the angle between the maximum radius of curvature of the talar head and a horizontal plane, as defined above. Ten specimens of each species plus the fossil casts were included.
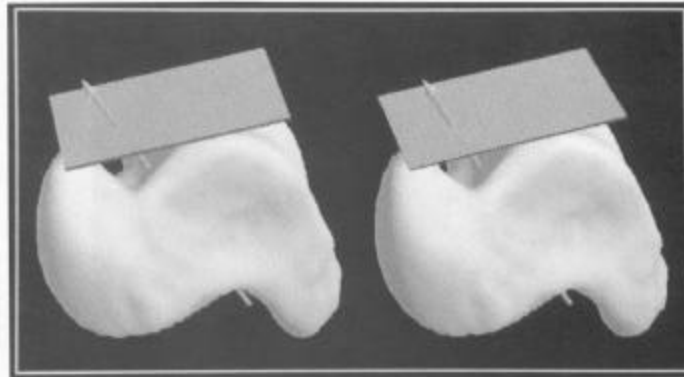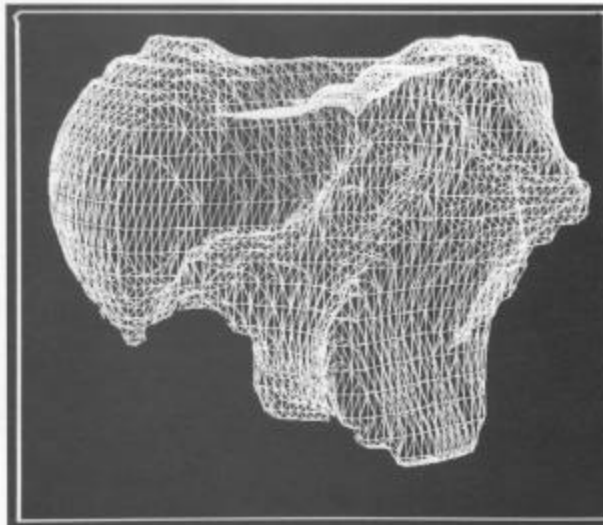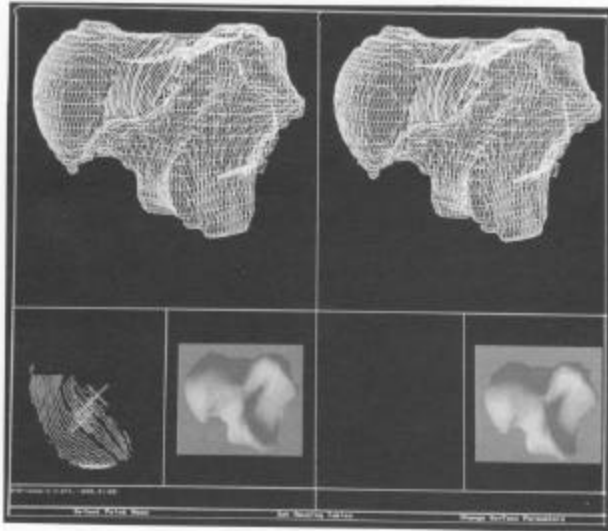
Fig. 4. – Stereo perspective of the view in Figure 3 (above) and the natural image (below). The elliptical slices through the sustentacular facets have been extracted and superimposed on one another (lower left). The cross represents the best fit center of the ellipses which was used to determine the axis in figures 2 and 5.
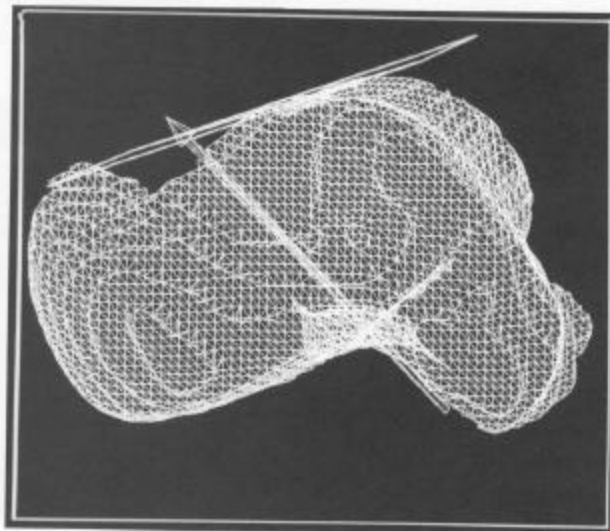

Fig. 5. – Medial view of a wire-frame image of the AL 288-1 talus. The orienting horizontal plane and estimated subtalar axis are indicated as in Figure 3.

RESULTS

At the calcaneocuboid articulation of the chimpanzee, a conical projection from the cuboid fits into a corresponding fossa on the calcaneus. Dorsally and laterally the bones contact on a flat surface. Rotation in supination/pronation is defined by the conical fit, while flexion requires separation of the flat surfaces. In the human foot, the joint is sellar in morphology but permits only a restricted gliding along either axis. The shape of the cuboid facet on the fossil calcanei (Olduvai and Omo) closely resembles the human condition.

The talonavicular joint is a modified ball-and-socket. The greatest radius of curvature is nearly horizontal in the chimpanzee but angled inferolaterally in the human. The computed angled differ significantly (fig. 6). The fossils, individually and collectively are significantly different from *Pan*, but not from *Homo*. The horizontal orientation seen in *Pan* corresponds to a lower placement of the head medial to the cuboid in such a manner as to permit midfoot flexion. The oblique position of the axis in hominids indicates a more dorsal position for the head, a greater habitual twist of the tarsal plate, and more restricted motion.

Fig. 6. – Orientation of the navicular facet on the talar head. A spread of one standard deviation is indicated for human and chimpanzee samples. Each of the hominid fossils is significantly different from *Pan* at p. 0.01.
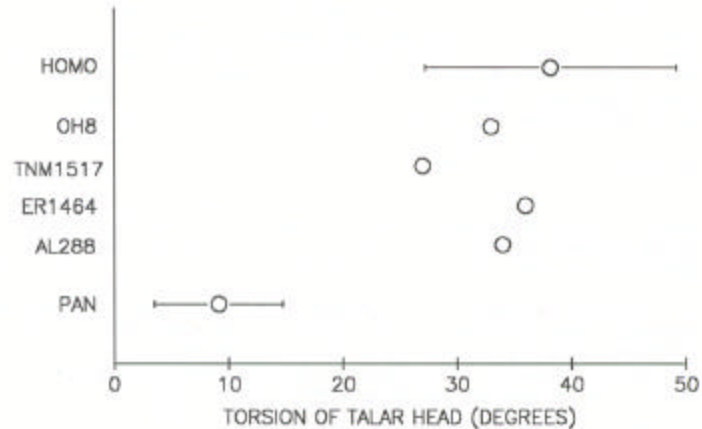
Manual manipulation of dry bones reveals that the chimpanzee talus can rotate on the subtalar facet with less disturbance of the talonavicular articulation. The facet on the head rotates parallel to its greatest radius of curvature, therefore neither realigning its axes nor substantially changing the position of the head relative to the calcaneocuboid articulation (fig. 1). Thus the mechanisms which immobilize the human transverse tarsal joint do not occur for the chimpanzee.

The computer imaging is currently being used to assess the subtalar articulation and to define its axis. The vector represented in fig. 2 is preliminary, as various strategies for fitting curves are being explored.

In addition to addressing the specific question of tarsal joint function, the imaging technique holds possibilities for direct morphological and kinesiological comparisons among living and extinct taxa, reconstructing missing complementary surfaces, predicting ranges of motion, and modeling hypothetical evolutionary pathways. These potentials remain for further exploration.

DISCUSSION

Our interpretation of the australopithecine tarsals (including *Homo habilis*) indicates that the arrangement of the transverse tarsal joint closely resembles the human condition. Probably the early hominid foot skeleton was morphologically capable of providing the distribution of pressure and the maintenance of balance that we associate with modern bipedalism. We now address the question of whether it also possessed a conversion mechanism and a functional medial longitudinal arch.

The factors responsible for locking the joints and elevating and maintaining the arch include the following :

1. An external rotation occurs along the entire lower limb, which translates as a lateral torque at both the ankle and subtalar joints. The resulting external rotation of the talus on the fixed tarsus causes supination in the peritalar joints.

2. Contraction of the *m.triceps surae* muscle inverts the calcaneus to further supinate the subtalar joint.

3. Ligaments about the talar head and in the plantar compartment tighten as a result of this supination. Body weight holds the talus in this position and effectively locks the medial row of pedal elements into a rigid chain.

4. The head of the talus is now relatively more superior with respect to the cuboid and its orientation has changed. These two factors prevent midfoot dorsiflexion.

5. Extrinsic and intrinsic plantar muscles actively contracting provide additional dynamic support.

6. The tendons of these muscles plus the plantar aponeurosis are passively further tensed in response to hyperextension of the toes ("windlass effect"), thus elevating the arch.

The bones of the early hominids and their articulations are, by our observations, consistent with appropriate motions at the peritalar joints, while muscle contraction and ligament tension cannot be directly assessed. The first two factors — rotation along the axis of the limb and triceps action — are important for initiating the supination that leads to close-packing. The torque is generated by horizontal rotation of the pelvis during stance phase and is amplified by the close placement of the foot to the midline and by increasing stride length. Near-midline foot placement is indicated in the fossils by the carrying angle of the femur. Furthermore the essentially human pattern of both foot placement and stride length are confirmed in the Laetoli footprints (Charteris *et al.*, 1982 ; Tuttle, 1985).

Therefore it is reasonable to reconstruct an external torque generated at the pelvis that is partially resolved, in a human-like pattern, with the subtalar joint of the foot. That torque produces a subtalar supination during the push-off phase of gait that is consistent with the formation of a medial longitudinal arch. This mechanical analysis is in agreement with the apparent arch in the Laetoli footprints (White and Suwa, 1987).

Although supination can be effected in the chimpanzee foot, particularly in an arboreal or grasping behavior, it does not result in a rigid packing of the bones. On the ground, the subtalar joint has more independence from the transverse tarsal joints because they are roughly parallel. The tarsal plate never twists to a degree comparable to that of a human. Therefore the arrangement of the talonavicular and calcaneocuboid joints and their axes does not inhibit midfoot flexion.

The form of the cuboid facet on the fossil calcanei and the angle of inclination of the talar heads indicate a human-like alignment of the bones that does preclude motion at these joints. Once the talar head supinates and close-packs in its socket, the transverse tarsal joint will be rigid.

This reconstruction of the early hominid foot supports much previously published evidence of extensive adaptations to bipedalism among the earliest hominids. Terrestrial bipedal behavior of the Plio-Pleistocene hominids is established beyond doubt by the Laetoli footprints, dated at 3.6 m. In addition, nearly every skeletal adaptation to bipedalism identified in modern humans is present to some degree in the australopithecines. Earliest known occurrences include (dates are from Tattersall *et al.*, 1988) :

a. lumbar curvature : STS 14, 2.5 M.a., but possibly absent in AL 288-1, 3.0 M.a. (Johanson *et al.*, 1982).

b. pelvic shortening and remodelling : AL 288-1, 3.0 M.a.

c. femoral carrying angle : AL 129-1a, 1c, 3.6 M.a.

d. reduction of toe length : AL 333-115, 3.3 M.a.

e. hyperextension at the metatarsophalangeal joints : AL 333-115, 3.3 M.a.

f. stabilization of the talocrural joints and reduction of accessory motion : AL 288-1, 3.0 M.a.

g. expansion of the heel process by the addition of a lateral process : AL 333-115, 3.3 M.a.

h. reduction of intertarsal mobility : AL 333, 3.3 M.a.

i. adduction of the hallux : Laetoli footprints, 3.6 M.a. ; AL 333-115, 3.3 M.a.

These adaptations for efficient bipedalism are not consistent with the climbing adaptations known from the feet of modern great apes. The adducted hallux and shortened toes significantly detract from the ability of a hominid to maintain a secure grasp on a tree limb. The large base of support produced by the rigid hominid tarsal plate would work at a disadvantage in an arboreal environment.

Upright posture and bipedalism are therefore the earliest traits that we consider distinctive of modern humans for which we have evidence. In contrast, all evidence for significant cultural advances occur later :

a. brain size expansion beyond an ape grade : *Homo* at East Turkana, ca. 2.0 M.a.

b. complex material culture : stone tools from Hadar, ca. 2.5 M.a. ; Olduvai Gorge, ca. 1.9 M.a.

c. altricial infancy and delayed maturation : presumably accompanying brain expansion.

d. complex social behavior, mating patterns : no unequivocal evidence before *Homo sapiens* (but such behavior is not likely to leave a clear record).

CONCLUSIONS

We have described a new tool for the investigation of early hominid functional anatomy. The potential applications for computer imaging and manipulation of the fossils extend to more complex reconstructions of incomplete material and their kinematic relationships.

The preliminary comparisons made in this paper argue that the pedal mechanics of *Australopithecus* include some of the crucial modern components of bipedal positional behavior, particularly in the ability of the foot to convert between a loose-packed and a close-packed chain of bones. The conversion mechanism and the resulting longitudinal arch represent a significant improvement in the efficiency of bipedal gait over that seen in non-human primates.

These inferences add to the accumulating evidence that the transition to bipedalism, with extensive morphological adaptations, occurred very early, perhaps before any other of the distinctive human traits. We interpret this to support the hypothesis that terrestrial bipedalism was the primary and original adaptation of the hominid lineage. Other behavioral characters evolved later and were not causal to bipedalism.

ACKNOWLEDGEMENTS

REFERENCES

BAKER H.H. (1988). – Building, visualizing, and computing on surfaces of evolution. *Computer Graphics and Applications*, 8, 31-41.

CHARTERIS J., WALL J.C. and NOTTRODT J.W. (1982). – Pliocene hominid gait : new interpretations based on available footprint data from Laetoli. *Am. J. Phys. Anthrop.*, 58, 133-144.

CLOSE J.R., INMAN V.T., POOR P.M. and TODD F.N. (1967). – The function of the subtalar joint. *Clin. Orthop.*, 50, 159-179.

ELFTMAN H. (1960). – The transverse tarsal joint and its control. *Clin. Orthop.*, 16, 41-46.

ELFTMAN H. and MANTER J. (1935). – Chimpanzee and human feet in bipedal walking. *Am. J. Phys. Anthrop.*, 20, 69-79.

FLEAGLE J.G., STERN J.T., JUNGERS W.J., SUSMAN R.L., VANGOR A.K. and WELLS J.P. (1981). – Climbing : a biomechanical link with brachiation and bipedalism. *Symp. Zool. Soc. London*, 48, 359-375.

GOULD S.J. (1989). – Contingency and prediction in the history of life. Paper presented at *History and Evolution*, 12th Annual Spring Systematics Symposium, Field Museum of Natural History : Chicago.

JOHANSON D.C., LOVEJOY C.O., KIMBEL W.H., WHITE T.D., WARD S.C., BUSH M.E., LATIMER B.M. and COPPENS Y. (1982). – Morphology of the Pliocene partial hominid skeleton (A.L. 255-1) from the Hadar Formation, Ethiopia. *Am. J. Phys. Anthrop.*, 57, 403-451.

JONES R.L. (1945). – The functional significance of the declination of the axis of the subtalar joint. *Anat. Rec.*, 93, 151-159.

LANCASTER J.B. (1978). – Carrying and sharing in human evolution. *Human Nature*, 1(2), 82-89.

LANGDON J.H. (1985). – Fossils and the origin of bipedalism. *J. Hum. Evol.*, 14, 615-635.

LOVEJOY C.O. (1981). – The origin of Man. *Science*, 190, 341-350.

TANNER (1981). – On becoming human. Cambridge University Press : Cambridge.

TATTERSALL I., DELSON E. and VAN COUVERING J. eds. (1988). – Encyclopedia of human evolution and prehistory. Garland Pub. : New York.

TUTTLE R.H. (1981). – Evolution of hominid bipedalism and prehensile capabilities. *In* : J.Z. Young, E.M. Jope, and K.P. Oakley eds., "The emergence of man", The Royal Society : London, 89-94.
(1985). – Ape footprints and Laetoli impressions : a response to the SUNY claims. *In* P.V. Tobias, ed. "Human evolution : past, present, and future", Alan R. Liss : New York, 129-133.

WHITE T.D. and SUWA G. (1987). – Hominid footprints at Laetoli : facts and interpretations. *Am. J. Phys. Anthrop.*, 72, 485-514.

Colloque International de la Fondation Singer-Polignac
(5-8 juin 1990)

ORIGINE(S) DE LA BIPÉDIE CHEZ LES HOMINIDÉS

Sous la direction de

Yves COPPENS et Brigitte SENUT