Polish Annals of Medicine

Journal homepage: https://www.paom.pl

Review paper

What made hominins physically active? Part I

Joanna Rutkowska-Talipska[1], Paweł Sowa[2], Krzysztof Rutkowski[3], Marcin Baltaziak[1], Tomasz Napiórkowski[4], Anna Kuryliszyn-Moskal[1], Ryszard Rutkowski[5]

[1] Department of Rehabilitation, Faculty of Health Sciences, Medical University of Bialystok, Poland
[2] Department of Population Medicine and Civilization Diseases Prevention, Faculty of Medicine, Medical University of Bialystok, Poland
[3] Department of Allergy, Guy's and St Thomas' NHS Foundation Trust, London, United Kingdom
[4] World Economy Research Institute, Collegium of World Economy, Warsaw School of Economics, Poland
[5] Department of Respiratory Diagnostic and Bronchoscopy, Medical University of Bialystok, Poland

ARTICLE INFO

Article history
Received 16 April 2018
Accepted 1 September 2018
Available online 21 November 2018

Keywords
Walking
Musculoskeletal system
Evolution
Hominins
Bipedality

Doi
https://doi.org/10.29089/2018.18.00064

User license
This work is licensed under a Creative Commons Attribution – NonCommercial – NoDerivatives 4.0 International License.

BY-NC-ND

ABSTRACT

Introduction: Understanding of the nature and timing of the transition to bipedal terrestrial locomotion is key to accurate interpretation of how and why humans evolved and improved their balance as well as reduced energy expenditure when moving upright.

Aim
We present an abbreviated history of the evolution of the musculoskeletal system in hominins, the role of bipedality and running in the genesis of pre-modern Homo.

Material and methods: The literature on this subject.

Results and discussion: Paleoantrhropological research traces the evolution of the hominins' skeleton and muscular system which allowed for strenuous bipedal, upright walking.

Conclusions
The complex evolutionary process of hominins' skeleton and muscular system resulted in new physical features and increased physical fitness

Corresponding author: Ryszard Rutkowski, Department of Respiratory Diagnostic and Bronchoscopy, Medical University of Bialystok, Waszyngtona 17, 15-274 Bialystok.
E-mail address: rutrys@gmail.com.

1. INTRODUCTION

Modern evolutionary research is a valuable contribution to medicine and health care practice.[1] It helps us to understand the role of musculoskeletal modifications in the shaping of human physical fitness. Fossil records make it possible to imagine how the morphology and biomechanics of our ancestors changed and turned us into physically active beings.[2–4] Insight into locomotor evolution from hominins (our ancestors back to the separation of the human and ape lineage) to *Homo sapiens* provides answers to the question about the therapeutic role of exercise in medicine and human adaptation to physical inactivity.[2,5–8] Evolutionary thinking helps us understand the link between current civilisation diseases epidemic and a dramatic mismatch between modern and Paleolithic levels of physical activity.[1,9,10] Evolutionary knowledge increases our chances of explaining why in the present ‘chair-based’ environment some of us became Fattyputs whilst others stay lean Thiniffers. Finally, evolutionary thinking might help prevent the morbidity related to the current pandemic of physical inactivity and sedentary lifestyle.[1,7,10]

2. AIM

We present an abbreviated history of the evolution of human musculoskeletal system from very early to transitional hominins. We focus on the role of bipedality in hominins’ survival and subsequent effective human walking. The evolution of the musculoskeletal system in *Homo species* and the invaluable role of physical activity in human health will be discussed in the second part of our review.[11]

3. DISCUSSION

The hominins underwent significant somatic, physiological and behavioural modifications from the divergence of the Pan-Homo’s last common ancestor and the very early primitive hominins (possible hominins or protohominins) about 8–6 million years ago (Ma) up to the last transitional hominins (Table).[1,5,6,8,12–14] The hallmark of hominins lineage was bipedality.[12,13] Recent fossil evidence makes it clear that bipedal gait appeared long before the formation of effective human thermoregulation, enlargement of the brain, acquisition of tool-making skills or emergence of language abilities.[13,15] It is believed that the ability to move in an orthograde position occurred for the first time in the oldest hominins: *Sahelantropus tchadensis*, *Orrorion tugenensis*, *Ardipithecus ramidus* and *kadabba* (Table).[5,6,16,17] There is not yet sufficient information to deduce reliably whether *Sahelantropus* was a biped. However, its basocranium had an anteriorly positioned and horizontally orientated foramen magnum, flat nuchal plane oriented at about 36° relative to the Frankfurt horizontal line and the nuchal crest lipping downward what suggests that it moved – at least occasionally – in an upright position.[9,16–19] Moreover, the paleoenvironment at the site where its remains were recovered seems to support this concept. About 7 Ma the Djurab desert in the northern Chad was a mosaic of damp, perilacustrine gallery forests, grassy savannah and woodlands.[6,9,16,17,19] *Sahelantropus tchadensis*’ movement within the tree crowns and climbing their trunks (‘vertical climbing’ hypothesis) forced a two-footed walk in an erect posture. Moreover, the abundance of lakes and rivers in *Sahelantropus*’ environment (‘shore dweller’ hypothesis) stimulated these protohominins to stand up or take steps in an upright position when wading in knee-deep water (’wading’ hypothesis).[6, 15] In the case of *Sahelantropus* one can only assume its bipedality. No such doubts exist in the

Table. Anthropometric characteristics of hominins.[5,8,9,13–15,23,24]

Informal groups	Representative taxa (*splitting taxonomy*)	Estimated age, y	Epoch	Cranial capacity (cc)	Body mass, kg Female–Male	Stature, cm	Development
Possible early hominins	*Sahelantropus tchadensis*	7.0–6.0 Ma	Late Miocene 11.6–5.3 Ma	~320–380	–	–	Arboreality, probable bipedality
	Orrorin tugenensis	6.2–5.6 Ma		–	35–50	110	Fit climber and clamber; not well adapted to longer bouts of terrestrial bipedality
	Ardipithecis ramidus kadabba	5.8–5.2 Ma		–	–	–	
	Ardipithecus ramidus	5.7–4.5 Ma		–	~ 40 - 50	120	
Archaic hominins	*Australopithecus anamensis*	4.1–3.5 Ma		–	–	–	Facultative, habitual terrestrial biped; more capable climbers than most modern humans (unclear arboreality)
	Australopithecus afarensis	3.6–3.0 Ma	Pliocene 5.3–2.6 Ma	438 (350–500)	29–45	110–130	
	Australopithecus africanus	3.0–2.6 Ma		457 (435–530)	36 (30–41)		
	Paranthropus boisei	2.2–1.2 Ma		510	44 (34–49)	155–160	
	Paranthropus robustus	2.0–1.5 Ma		515 (500–530)	–	–	
Transitional hominins	*Australopithecus habilis* or *Homo habilis sensu stricto*	2.3–1.6 Ma	Pleistocene 2.6 Ma – 100 Ka	601 (552–612)	34 (32–37)	–	
	Homo rudolfensis	2.4–1.8 Ma		753	56–60	–	

Comments: Ma – million years ago; Ka – thousand years ago.

case of Orrorins (*O. tugenensis*), which, when on the ground, habitually or perhaps even obligatorily moved on the hind limbs. Its anatomy substantiates this claim. The proximal part of femur is oval in cross-section and has a spherical, slightly anteriorly rotated head connected with an elongated neck, which is a feature of bipedal creatures. Orrorins were adapted to arboreality: a pronounced humeral vertical brachioradialis crest and curved, proximal manual phalanx suggest that it climbed trees to forage, build shelter (nests), seek refuge and escape predators.[6,9,15,17,19] Further changes which improved hominins' locomotion occurred 5.5–4.5 Ma in *Ardipithecus*.[6,20–23] It, just like Orrorins, lived in wet, woodland/forest habitats and had to preserve both the ability of arboreal and terrestrial locomotion.[22,24] The former was effective thanks to robust arms and legs of about equal length, ape-like feet structure with curved toes and a grasping, fully opposable hallux.[9,19,22,23] *Ardipithecus* – the oldest reliably described hominin – improved its upright locomotion with extended hip and knee thanks to some new characteristics of the foot and pelvis and despite retained hallucial grasping and a primitive elongate ischium still required for climbing. Its hallux retained its opposability, but the lateral phalanges took on the primary role of terrestrial propulsion, as shown by a tendency for a hypertrophied second phalanx and an *Australopithecus* – like dorsally developed lateral metatarsal head. Thanks to these changes *Ardipithecus* was able to use its lateral foot as an effective lever for 'toe-off' during bipedal progression.[12,19,21,24,25] Its pelvis was remodeled to allow for terrestrial bipedality and effective balance control during upright walking. The upper part was dramatically shortened especially in the distance from the sacral articulation to the hip joint and become wider with lower iliac flares, which elongated the waist and made the trunk more elastic and better cushioned the side body movements.[24,25] *Ardipithecus* could not walk particularly well and was not as well-adapted to long, strenuous bouts of terrestrially bipedality as the species that followed. Its feet were still stiff due to a thick plantar layer of fibrous tissue and lack of elastic medial longitudinal and transverse arches; upper limbs were almost equal length to hind limbs which impeded swing symmetry of the upper and lower limbs and hampered its gait.[19,24] Between 4.5 MA and 1.9 Ma human-like, upright two-footed gait appeared for the first time in *Australopithecus* genus in Africa (Table).[20,26] Around 3–2 Ma, there were diametrical climate changes due to glaciation of the northern hemisphere and decreasing intensity of monsoon rains, humidity and forest and tree areas in Africa. Large grassy savannahs appeared in and nearby the East African Rift Valley, which extends from today's Ethiopia to the Republic of South Africa. In order to survive, *Australopithecus*' skeleton underwent changes, which, compared with *Ardipithecus*, improved its bipedal walk.[12] It was significantly more mobile than *Sahelanthropus*, *Orrorin* and *Ardipithecus* so could walk for long distances.[14,21,26] A new spinal and pelvic anatomy improved its ability to walk even further. The tall *Au. Africanus*' waist increased the distance between the ribs and pelvis decoupling the thorax and hips, enhancing body flexibility in the abdominal segment and allowing for more trunk rotation. Iliac blades shortened vertically and moved laterally out over the hip joints and femoral neck creating a wider pelvis which allowed for a more forward movement of the lower limbs for each degree of rotation and increased stride length during the walk of these short-legged bipeds. Additional changes to the upper part of its pelvis facilitated the development of lumbar lordosis at L5/S1 and improved the position of the gluteal muscles. This improved the balance of the upper body during walking and reduced energy expenditure when standing erect or moving upright. The gluteal muscles became the principal stabilizers of the trunk effectively controlling forward rotation of the trunk at ground contact and minimizing walking fatigue.[19,27–29] Elongated femur enhanced the inverted pendulum mechanism of walking, which allowed for a better retrieval of the energy created during active movement on the ground. Further reduction in energy expenditure during a long march was possible because of lack of an opposable big toe, the calacaneal bone expansion and appearance of a form of elastic, energy saving plantar arches in its foot.[12,26,30] Australopiths gait was still stiff-legged, different from human locomotion; legs were short but arms relatively long what undoubtedly facilitated tree climbing, but hampered arm swing during terrestrial walk. Achilles tendons were lacking or poorly developed so its spring and running mechanism was limited. Its gluteal muscles were less developed, longitudinal arch of the foot was not fully shaped and the toes were long and curved, which made it harder to walk smoothly on the ground; quick and long-lasting running was impossible.[31–33]

4. CONCLUSIONS

Australopithecines' fully acquired bipedality and upright position allowed for more effective walking over long distances. That ability of bipedal walk induced further somatic improvements in the genus *Homo* making him an effective, obligate terrestrial biped and endurance runner, well-adapted to the changing climate and paleoenvironment.[3,4,6,15] This in turn accelerated the pace of evolution of the human species which we describe in more detail in the second part of our review.[11]

Conflict of interest
None declared.

Funding
None declared.

References

1. Varki A. Nothing in medicine makes sense, except in the light of evolution. *J Mol Med (Berl)*. 2012;90(5):481–494. https://doi.org/10.1007/s00109-012-0900-5.
2. Kirchengast S. Bone loss and physical activity – a bio anthropological perspective. *J Osteopor Phys Act.* 2015;4(1):164. https://doi.org/10.4172/2329-9509.1000164.

3 Ward CV. Interpreting the posture and locomotion of Australopithecus afarensis: where do we stand? *Am J Phys Anthropol*. 2002;Suppl 35:185–215.

4 Preuschoft H. Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture? *J Anat*. 2004;204(5):363–384. https://doi.org/10.1111/j.0021-8782.2004.00303.x.

5 Carroll SB. Genetics and the making of Homo sapiens. *Nature*. 2003;422(6934):849–857. https://doi.org/10.1038/nature01495.

6 Crompton RH, Vereecke EE, Thorpe SK. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *J Anat*. 2008;212(4):501–543. https://doi.org/10.1111/j.1469-7580.2008.00870.x.

7 Levine JA. Lethal sitting: homo sedentarius seeks answers. *Physiology (Bethesda)*. 2014;29(5):300–301. https://doi.org/10.1152/physiol.00034.2014.

8 Wood B. Reconstructing human evolution: achievements, challenges, and opportunities. *Proc Natl Acad Sci U S A*. 2010;107(Suppl 2):8902–8909. https://doi.org/10.1073/pnas.1001649107.

9 Elton S. The environmental context of human evolutionary history in Eurasia and Africa. *J Anat*. 2008;212(4):377–393. https://doi.org/10.1111/j.1469-7580.2008.00872.x.

10 Lieberman DE. Is Exercise Really Medicine? An Evolutionary Perspective. *Curr Sports Med Rep*. 2015;14(4):313–319. https://doi.org/10.1249/JSR.0000000000000168.

11 Rutkowska-Talipska J. Sowa P, Rutkowski K, Baltaziak M, Napiórkowski T, Kuryliszyn-Moskal A, Rutkowski R. What made us physically active? Part II. *Pol Ann Med*. [in print]. https://doi.org/10.29089/2018.18.00065.

12 D'Aouit K, Aerts P. The evolutionary history of the human foot. In: D'Aout K, Lescrenier K, Van Gheluwe D, et al., eds. *Advances in plantar pressure measurements in clinical and scientific research*. Maastricht: Shaker Publishing BV,2008:44–68.

13 Malina RM. Physical activity in early and modern populations: an evolutionary view. In: Malina RM, Eckert HM, eds. *Physical Activity in Early and Modern Populations* (American Academy of Physical Education Papers 21), Champaign: Human Kinetics; 1988:1–12.

14 Robson SL, Wood B. Hominin life history: reconstruction and evolution. *J Anat*. 2008;212(4):394–425. https://doi.org/10.1111/j.1469-7580.2008.00867.x.

15 Niemitz C. The evolution of the upright posture and gait – a review and a new synthesis. *Naturwissenschaften*. 2010;97(3):241–63. https://doi.org/10.1007/s00114-009-0637-3.

16 Brunet M, Guy F, Pilbeam D, et al. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*. 2002;418(6894):145–151. https://doi.org/10.1038/nature00879.

17 Brunet M. Two new Mio-Pliocene Chadian hominids enlighten Charles Darwin's 1871 prediction. *Philos Trans R Soc Lond B Biol Sci*. 2010;365(1556):3315–3321. https://doi.org/10.1098/rstb.2010.0069.

18 Zollikofer CPE, Ponce de Leon MS, Lieberman DE, et al. Virtual reconstruction of Sahelanthropus tchadensis. *Nature*. 2005;434(7034):755–759. https://doi.org/10.1038/nature03397.

19 Brooks AS. New perspectives on the evolution of bipedalism. *Anthro Notes*. 2010;31(1):19–22. https://doi.org/10.5479/10088/22449.

20 Haile-Selassie Y, Melillo SM, Su DF. The Pliocene hominin diversity conundrum: Do more fossils mean less clarity? *Proc Natl Acad Sci USA*. 2016;113(23):6364–6371. https://doi.org/10.1073/pnas.1521266113.

21 Crompton RH, Sellers WI, Thorpe SK. Arboreality, terrestriality and bipedalism. *Philos Trans R Soc Lond B Biol Sci*. 2010;365(1556):3301–3314. https://doi.org/10.1098/rstb.2010.0035.

22 Lovejoy CO. Reexamining human origins in light of Ardipithecus ramidus. *Science*. 2009;326(5949):74e1-8. https://doi.org/10.1126/science.1175834.

23 White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G. Ardipithecus ramidus and the paleobiology of early hominids. *Science* 2009;326(5949):75–86. https://doi.org/10.1126/science.1175802.

24 White TD, Lovejoy CO, Asfaw B, Carlson JP, Suwa G. Neither chimpanzee nor human, Ardipithecus reveals the surprising ancestry of both. *Proc Natl Acad Sci USA*. 2015;112(16):4877–4884. https://doi.org/10.1073/pnas.1403659111.

25 Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. The pelvis and femur of Ardipithecus ramidus: the emergence of upright walking. *Science*. 2009;326(5949):71e1–6. https://doi.org/10.1126/science.1175831.

26 Maslin MA, Brierley CM, Milner AM, Shultz S, Trauth MH, Wilson KE. East African climate pulses and early human evolution. *Quart Sci Rev*. 2014;101:1–17. https://doi.org/10.1016/j.quascirev.2014.06.012.

27 Gruss LT, Schmitt D. The evolution of the human pelvis: changing adaptations to bipedalism, obstetrics and thermoregulation. *Philos Trans R Soc Lond B Biol Sci*. 2015;370:20140063. https://doi.org/10.1098/rstb.2014.0063.

28 Roach NT, Venkadesan M, Rainbow MJ, Lieberman DE. Elastic energy storage in the shoulder and the evolution of high-speed throwing in Homo. *Nature*. 2010;498(7455):483–486. https://doi.org/10.1038/nature12267.

29 Lovejoy CO. The natural history of human gait and posture. Part 1. Spine and pelvis. *Gait Posture*. 2005;21(1):95–112. https://doi.org/10.1016/j.gaitpost.2004.01.001.

30 Lieberman DE, Bramble DM. The evolution of marathon running: capabilities in humans. *Sports Med*. 2007;37(4–5):288. https://doi.org/10.2165/00007256-200737040-00004.

31 Lieberman DE, Bramble DM, Raichlen DA, Shea JJ. Brains, brawn, and the evolution of human endurance running capacities. In: Grine FE, Fleagle JG, Leakey RE, eds. *The First Human – Origin and Early Evolution of the Genus Homo*. Vertebrate Paleobiology and Paleoanthropology series. New York: Springer; 2009:77–92. https://doi.org/10.1007/978-1-4020-9980-9_8.

32 Lieberman DE, Raichlen DA, Pontzer H, Bramble DM, Cutright-Smith E. The human gluteus maximus and its role in running. *J Exp Biol*. 2006;209(Pt 11):2143–2155. https://doi.org/10.1242/jeb.02255.

33 McKeon PO, Hertel J, Bramble D, Davis I. The foot core system: a new paradigm for understanding intrinsic foot muscle function. *Br J Sports Med*. 2015;49(5):290. http://dx.doi.org/10.1136/bjsports-2013-092690.