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Steven L. Forman,
Baylor University, United States

*CORRESPONDENCE
Rita Sorrentino,
rita.sorrentino2@unibo.it
Nicholas B. Holowka,
nbholowk@buffalo.edu
Kristian J. Carlson,
kristian.carlson@usc.edu

†These authors have contributed equally to this work

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Editorial: Human upright walking from past to present

Rita Sorrentino[1*†], Nicholas B. Holowka[2*†] and Kristian J. Carlson[3,4*†]

[1]Department of Biological, Geological and Environmental Sciences—Bigea, University of Bologna, Bologna, Italy, [2]Department of Anthropology, University at Buffalo, Buffalo, NY, United States, [3]Department of Integrative Anatomical Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, United States, [4]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

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Editorial on the Research Topic
Human upright walking from past to present

Upright walking is a hallmark trait distinguishing humans from other primates. Although bipedalism has a central role in human evolution, when, how, and under what selective pressures it evolved remain long-standing questions (DeSilva et al., 2019; Holowka and Lieberman, 2018). Musculoskeletal adaptations of early hominins suggest they balanced an arboreal lifestyle, including climbing, with a terrestrial lifestyle, featuring bipedalism (Carlson et al., 2021; Prang, 2019; Sorrentino et al., 2023; Williams et al., 2023). While there are undoubtedly multiple adaptive solutions for achieving this balance, bipedalism eventually became the predominant hominin locomotor mode after the emergence of genus *Homo* (Bramble and Lieberman, 2004; Pontzer, 2017). Variations in morphology and bipedal gait mechanics can be heavily influenced by mobility, which in humans is partly a function of subsistence economy, substrate use, choice of footwear, and other biological factors (e.g., sex, age, and body mass) (Carlson and Marchi, 2014; Chirchir et al., 2015; Saers et al., 2019; Sorrentino et al., 2020; Trinkaus, 2005). While documenting the extent of 'normal' anatomical variation in human lower limb and foot morphology, and contextualizing its basis in human bipedal gait kinematics, continue to receive attention (Carlson et al., 2007; Hollander et al., 2017; Holowka et al., 2022; Thompson and Zipfel, 2005), morphological outcomes of gait adjustments are increasingly scrutinized (Uddin et al., 2020; Zhang et al., 2017).

This Research Topic consists of 10 peer-reviewed Original Research articles that contribute to our knowledge of the evolution of human bipedalism, and how bipedalism is linked to anatomical variation in modern humans and our close relatives from past to present (Figure 1).

Extant ape models have been recruited to frame selective forces driving the evolution of bipedalism in the last common ancestor of humans and chimpanzees. Sarringhaus et al. observed that chimpanzees use bipedal postures in arboreal settings primarily during feeding, whereas bipedalism was adopted on the ground during numerous contexts including aggressive interactions. They remind us that selective pressures at the origins of hominin bipedalism may be multifactorial rather than singular in cause. Locomotor

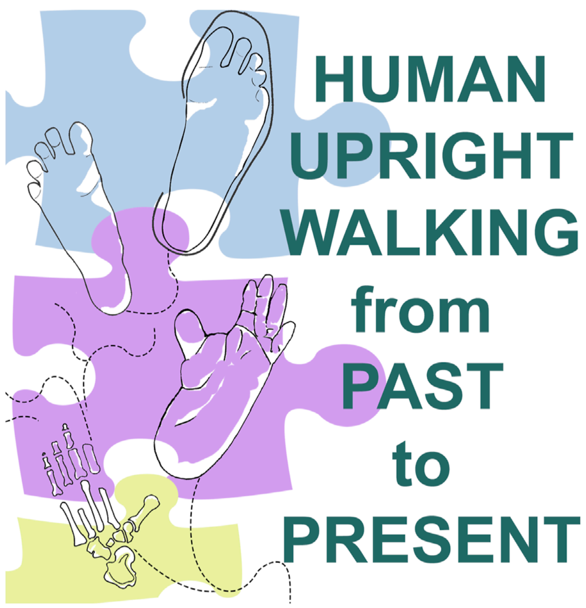

FIGURE 1
This Research Topic adds a piece to the puzzle of tracking the evolution of bipedalism.

behaviors of chimpanzees and gorillas shift during ontogeny. Saers highlights how age-related changes can be tracked in postcranial bone parameters within and between ape species. Specifically, he observes ontogenetic trends in relative bone density, i.e., diminishing in upper limb bones and increasing in lower limb bones, mirroring rising frequencies of terrestrial quadrupedalism approaching adulthood. Not only hard tissue structures track behavioral changes, but so do soft tissue structures. Warrener focuses on how muscles, specifically their scaling patterns, reflect differences in ape locomotor behaviors. She observes greater positive allometry in human hind limb muscles than has been reported in other apes, potentially reflecting human adaptations to bipedalism.

Kinematics and musculoskeletal modeling of human bipedalism provide opportunities to infer locomotor experimentation in early hominin ancestors. Zeininger et al. investigate how children's and adults' feet interact with substrates, focusing on ankle joint torques. Adults using a heel strike show more variable gearing than children with an immature foot strike. The authors attribute this to anatomical and motor control differences between juvenile and adult feet, and suggest selective benefits of variable gearing may have appeared around two million years ago with the emergence of a fully (adult-like) modern foot. Murray et al. use an OpenSim computational model to explore how lower limb bone curvature affects hominin locomotion. Different combinations of tibial and femoral curvature have distinct influences on muscle recruitment during uphill walking (stair climbing), suggesting adaptive differences exist between them. The authors revisit functional interpretations of long bone curvature in humans and Neanderthals, emphasizing the dynamic nature of different structural adaptations.

Through expressing form-function relationships in foot bones, obligate bipedalism in *Homo* manifests biomechanical challenges related to biological variables and mobility strategies (e.g., sex, age, footwear, levels of mobility). Figus et al. investigate the role of developmental age in the transformation of internal morphology and external configuration of the human talus. They observe plastic morphological and configurational changes during early childhood upon achievement of mature bipedal locomotion, and again during late adolescence potentially due to additional factors such as body mass increases. Plastic shape change also can occur in adult skeletal elements. Harper analyzes the effect of activity levels and footwear on the calcaneus, finding that form varies between sedentary and non-sedentary modern populations, with hunter-gatherers exhibiting a superoinferiorly taller and mediolaterally wider calcaneal tuber. This adaptive response is attributed to higher activity levels and less rigid footwear. Dann et al. analyze sexual dimorphism in calcaneal proportions of populations from the Levant during the Late Pleistocene to the early Holocene. Paleolithic *H. sapiens* exhibit calcanei better adapted for high mobility independent of sex, while sex-specific adaptations begin to appear with the transition to sedentary lifestyles.

An emerging research thread in evolutionary biomechanics is the assessment of interventional or corrective measures for abnormalities or pathologies in modern human walking gaits and foot mechanics. In a 5-month follow-up study design, Allen et al. demonstrate that custom-fit 3D-printed footwear modeled after a minimalist type of indigenous footwear does not significantly change peak pressure distribution compared to barefoot walking. The customized footwear significantly increases toe strength, however, and alters center-of-pressure (COP) patterns during gait, slowing COP movement in early and mid-stance compared to barefoot subjects. Alsenoy et al. evaluate different materials in custom foot orthoses to examine their influences on lower limb joint kinematics. Greater effects are observed in the ankle than in proximal joints, with harder materials causing more pronounced changes. Combining hard (in the heel) and soft (in the forefoot) materials in orthoses induces the most favorable changes in joint kinematics compared to shod subjects without orthoses.

Articles in this Research Topic cross-link disciplines, most notably Paleoanthropology, Primatology, Biological Anthropology, Orthopedics, Comparative Anatomy, Biomechanics, Functional Morphology, Skeletal Biology, and Kinesiology. This is intentional. The editors endorse a pluralistic approach to examining research questions, namely, utilizing a range of methodologies and interdisciplinary analyses to investigate bipedalism across different periods of human evolutionary history.

Author contributions

RS: Conceptualization, Methodology, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. NH: Conceptualization, Methodology, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. KC: Conceptualization, Methodology, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing.

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Conflict of interest

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References

Bramble, D. M., and Lieberman, D. E. (2004). Endurance running and the evolution of Homo. *Nature* 432, 345–352. doi:10.1038/nature03052

Carlson, K. J., Green, D. J., Jashashvili, T., Pickering, T. R., Heaton, J. L., Beaudet, A., et al. (2021). The pectoral girdle of StW 573 ('Little Foot') and its implications for shoulder evolution in the Hominina. *J. Hum. Evol.* 158, 102983. doi:10.1016/j.jhevol.2021.102983

Carlson, K. J., Grine, F. E., and Pearson, O. M. (2007). Robusticity and sexual dimorphism in the postcranium of modern hunter-gatherers from Australia. *Am. J. Phys. Anthropol.* 134, 9–23. doi:10.1002/ajpa.20617

Carlson, K. J., and Marchi, D. (2014). *Reconstructing mobility: environmental, behavioral, and morphological determinants*. New York: Springer.

Chirchir, H., Kivell, T. L., Ruff, C. B., Hublin, J., Carlson, K. J., Zipfel, B., et al. (2015). Recent origin of low trabecular bone density in modern humans. *Proc. Natl. Acad. Sci. U. S. A.* 112, 366–371. doi:10.1073/pnas.1411696112

DeSilva, J., McNutt, E., Benoit, J., and Zipfel, B. (2019). One small step: a review of Plio-Pleistocene hominin foot evolution. *Am. J. Phys. Anthropol.* 168, 63–140. doi:10.1002/ajpa.23750

Hollander, K., de Villiers, J. E., Sehner, S., Wegscheider, K., Braumann, K.-M., Venter, R., et al. (2017). Growing-up (habitually) barefoot influences the development of foot and arch morphology in children and adolescents. *Sci. Rep.* 7, 8079. doi:10.1038/s41598-017-07868-4

Holowka, N. B., Kraft, T. S., Wallace, I. J., Gurven, M., and Venkataraman, V. V. (2022). Forest terrains influence walking kinematics among indigenous Tsimane of the Bolivian Amazon. *Evol. Hum. Sci.* 4, e19–e17. doi:10.1017/ehs.2022.13

Holowka, N. B., and Lieberman, D. E. (2018). Rethinking the evolution of the human foot: insights from experimental research. *J. Exp. Biol.* 221, jeb174425. doi:10.1242/jeb.174425

Pontzer, H. (2017). Economy and endurance in human evolution. *Curr. Biol.* 27, R613–R621. doi:10.1016/j.cub.2017.05.031

Prang, T. C. (2019). The African ape-like foot of Ardipithecus ramidus and its implications for the origin of bipedalism. *Elife* 8, e44433. doi:10.7554/elife.44433

Saers, J. P. P., Ryan, T. M., and Stock, J. T. (2019). Trabecular bone functional adaptation and sexual dimorphism in the human foot. *Am. J. Phys. Anthropol.* 168, 154–169. doi:10.1002/ajpa.23732

Sorrentino, R., Carlson, K. J., Orr, C. M., Pietrobelli, A., Figus, C., Li, S., et al. (2023). Morphological and evolutionary insights into the keystone element of the human foot's medial longitudinal arch. *Commun. Biol.* 6 (1), 1061. doi:10.1038/s42003-023-05431-8

Sorrentino, R., Stephens, N. B., Carlson, K. J., Figus, C., Fiorenza, L., Frost, S., et al. (2020). The influence of mobility strategy on the modern human talus. *Am. J. Phys. Anthropol.* 171, 456–469. doi:10.1002/ajpa.23976

Thompson, A. L. T., and Zipfel, B. (2005). The unshod child into womanhood – forefoot morphology in two populations. *Foot* 15, 22–28. doi:10.1016/j.foot.2004.10.002

Trinkaus, E. (2005). Anatomical evidence for the antiquity of human footwear use. *J. Archaeol. Sci.* 32, 1515–1526. doi:10.1016/j.jas.2005.04.006

Uddin, K. Z., Youssef, G., Trkov, M., Seyyedhosseinzadeh, H., and Koohbor, B. (2020). Gradient optimization of multi-layered density-graded foam laminates for footwear material design. *J. Biomechanics* 109, 109950. doi:10.1016/j.jbiomech.2020.109950

Williams, S. A., Prang, T. C., Russo, G. A., Young, N. M., and Gebo, D. L. (2023). African apes and the evolutionary history of orthograde and bipedalism. *Am. J. Biol. Anthropol.* 181, 58–80. doi:10.1002/ajpa.24684

Zhang, X., Li, B., Hu, K., Wan, Q., Ding, Y., and Vanwanseele, B. (2017). Adding an arch support to a heel lift improves stability and comfort during gait. *Gait Posture* 58, 94–97. doi:10.1016/j.gaitpost.2017.07.110