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Citation (please note it is advisable to refer to the publisher’s version if you intend to cite from this work)

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A RE-ANALYSIS OF CHIBANIAN PLEISTOCENE TRACKS FROM VÉRTESSZŐLŐS, HUNGARY, EMPLOYING PHOTOGRAMMETRY AND 3D ANALYSIS

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Tanaka, I., Markó, A., Hyodo, M., Strickson, C. E. & Falkingham, P. L., 2021. A re-analysis of Chibanian Pleistocene tracks from Vértesszőlős, Hungary, employing photogrammetry and 3D analysis. Annales Societatis Geologorum Poloniae, 91: xx–xx.

Abstract: The Vértesszőlős quarry, the Palaeolithic site where the “Samu” hominin fossil remains (Homo heidelbergensis) were found, is located in North West Hungary. The site is dated between the Early and Middle Pleistocene (ca. 310 ka). A short distance from where the Samu remains were found is an exposed surface of calcareous mudstone, preserving numerous fossil tracks made by a range of mammals and birds. Of particular interest are three elongate impressions - two potentially successive and one isolated. These tracks have previously been referred to either hominin or ursine trackmakers. Since bear pes tracks can superficially resemble human tracks, we attempted to discern the 3D morphology of the traces using digital photogrammetry. Our analysis suggests the isolated impression is likely the product of two superimposed tracks of a cloven hoofed ungulate. However, the two potentially successive tracks are more problematic. The highly weathered surface (first exposed in the 1960’s) has made interpretation difficult. Both impressions seem to possess a narrow, rounded end similar to the posterior heel margin of a human track. At the anterior end the impressions are broader, and bounded by smaller impressions that could be interpreted as toe marks. However, these two tracks differ considerably in their length/width ratios and are too widely spaced to be part of a single bipedal trackway. It is conceivable that one or both of these impressions may be highly weathered hominin tracks. However, given the highly weathered nature of the exposed surface, and the lack of morphological detail in the tracks, we cannot at this time confidently attribute the tracks to any specific trackmaker, despite our digital models of the tracks which provide a relatively objective means of analysis independent of prior assumptions.

Key words: Pleistocene, Palaeolithic site, calcareous mudstone, mammal track, comparative ichnology.

Manuscript received 4 May 2020, accepted 1 January 2021

INTRODUCTION

The analysis of human and animal tracks in archaeological and palaeontological contexts can provide information about the composition of local fauna that would otherwise be unavailable from body fossils alone (e.g., Falkingham, 2014; Lallensack et al., 2015; Helm et al., 2020). However, identifying trackmakers remains a difficult task, especially for morphologically similar ichnotaxa (e.g., Lucas and Hunt, 2007; Klein and Lucas, 2015; Ledoux and Boudade-Maligne, 2015; Buchwitz and Voigt, 2018; Buckley et al., 2018). In some substrates, sediment collapse and flow exacerbate the difficulty in identifying tracks. For example, human feet can often leave an elongated shape with no distinct toe impressions (e.g., Marty et al., 2009; Bennet and Morse, 2014; Marchetti et al., 2020). In such cases, identification relies on successive tracks, and thus a given track may be identified as hominin from context of trackways, rather than...
from isolated tracks (e.g., Mietto et al., 2003; Lockley et al., 2008; Bennet and Morse, 2014). Other terrestrial mammals, e.g., bears and bovids, have also been known to leave elongated tracks on occasion, either as the result of an elongate foot, or through a complex interaction of quadrupedal over-stepping (Elbroch, 2003; McDougall, 2015). Consequently, human tracks, even when shod, can in some circumstance leave tracks of a similar shape to those left by bears and bovids (Gierliński et al., 2017). We collected, from soft muddy substrates, digital images of bovid and bear tracks of similar size to human tracks, to be compared with the fossil tracks from Vértesszőlős, Hungary.

The purpose of this study is to re-analyse three tracks previously regarded either as being produced by Ursus stehlini (Kretzoi) (small bear) (Kretzoi and Dobosi, 1990) or as produced by hominins (Vértes, 1964). Throughout the analysis, we combine standard visual descriptions with 3D digitization methods, in order to objectively describe these tracks.

**GEOLOGICAL SETTING**

The Vértesszőlős freshwater limestone quarry (N47.63, E18.38) is located in the northwestern part of Hungary, in the Western foothills of the Transdanubian mountains (Fig. 1). Quarry excavations were operated by the project team of Dr. László Vértes during the 1960s. The Vértesszőlős site is known for fossils of Homo heidelbergensis (Stringer, 2012), Palaeolithic tools (Dobosi, 2003), and several mammal skeletal remains (e.g., horse, bullocks, bison, bear, rhinoceros, stag and rodent) (Kretzoi and Vértes, 1965).

The Quaternary sediments of the quarry represent fluviatil (sand, gravel), aeolian (loess, sand) and freshwater limestone deposits (Haas, 2013; Fig. 2). Within the quarry, 8 sites have been excavated (Fig. 3). Fossil tracks have previously been reported from site III and attributed to mammals such as Ursus, Stephanorhinus, Capreolus and Megaloceros (Kretzoi and Dobosi, 1990). Site III has also yielded lithic tools from the palaesurface above the tracks, but no hominid and mammalian skeletal remains have been found here. The trace fossils are preserved in calcareous mudstone which has been dated to 310±30ka using Th$^{230}$/U$^{234}$ (Kele et al., 2016; Fig. 2). This constrains the tracksite at approximately the same age as the deposits from which the Homo remains were uncovered at site I, which have been dated to 315±72ka using a radiosiotopic method (Th$^{230}$/U$^{234}$; Kele et al., 2016).

The track site (site III) is now protected as an open-air museum, as part of the Vértesszőlős Hungarian National Museum. The site III extends approximately 40 m², and the trampled surface is on a laminated calcareous mudstone layer (itself partly overlain by a tuffaceous calcareous mudstone). The record consists of 125 tracks, 106 of which identified as produced by mammals (e.g., bison, bear, rhinoceros and stag) and some others attributed to avian trackmakers (Kretzoi and Dobosi, 1990). There are three elongated tracks (one isolated and two possibly associated), previously attributed to Ursus stehlini (small bear), and interpreted as a left manus imprint and a right pes imprint (Kretzoi and Dobosi, 1990; Fig. 4).

![Geographical location of the Vértesszőlős quarry, Hungary (marked with a star).](image-url)
METHODS

Collecting tracks of extant taxa

We used photographs of manus and pes tracks of two Asian black bears (*Ursus thibetanus* Cuvier), that were provided by Mr. Yoshiaki Okamura, one from the Shiga prefecture, and the other from the Ishikawa prefecture, Japan. Photographs of tracks from four bovid species were also provided by Mr. Yoshiaki Okamura:

- Indian bison (*Bos gaurus* (Smith)) from Khao Yai National park, Thailand,
- Asian water buffalo (*Bubalus arnee* (Keer)) from northern Thailand,
- Asian water buffalo (*Bubalus arnee*) from Koshi Tappu Wildlife camp, Nepal, and
- aurochs (*Bos primigenius indicus*) from northern Thailand.

Additionally, photographs of two human tracks from actualistic experimental studies (I. Tanaka and M. Tanaka as trackmakers) and made in mud and sand were used (Fig. 5).

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**Fig. 2.** Lithological log of Sites I and III. Track layer found in alternating calcareous mudstone (travertine), and calcareous tuff (travertine). Dates included are from Hennig *et al.* (1983) and Kele *et al.* (2016). The grey ones show the estimated time by ESR method in Hennig *et al.* (1983).
Fig. 3. Map of the Vértesszőlős quarry, with previous sites and finds labelled. Site I: osteological material of *Homo heidelbergensis* and other mammals, and tools. Site II: osteological mammal remains and tools. Site III (focus site of this study): Tracks attributed to mammals and birds. Reproductive by Kretzoi and Dobosi (1990).

Fig. 4. Interpretive map of the track surface at site III (modified from Kretzoi and Dobosi, 1990). The black track sketches, numbered 1–3, are those previously interpreted as being made by a small bear and analysed in detail here.
Fig. 5. Comparative tracks from extant taxa. A. *Bos gaurus* (the manus is overlapped by the pes) in mud substrate. B. *Bubalus arnee* in mud substrate. C. *Bubalus arnee* in muddy-sandy substrate. D. *Bos primigenius indicus*, plaster cast, convex hyporelief. E. *Ursus thibetanus*, plaster cast, convex hyporelief (left manus imprint and right pes imprint). F. *Ursus thibetanus* (right manus) in clay. G. *Ursus thibetanus* in clay (left pes). H. Manus and pes of *Ursus thibetanus*. I. Right pes track of *Homo sapiens* in moist, coarse- to medium-grained substrate. J. Right pes track of *Homo sapiens* in moist, medium- to fine-grained substrate. White arrows in A–D show the edge of hooves, and in Figure C also point to the dew claw. Photographs in A–H by courtesy of Mr. Yoshiaki Okamura.
Photogrammetric digitization at Vértesszőlős

The elongated fossil tracks from Hungary were digitized using photogrammetry (Falkingham, 2012; Mallison and Wings, 2014; Falkingham et al., 2018), albeit post-hoc (i.e. photos were taken prior to considering the application of photogrammetry, e.g., Falkingham et al., 2014, 2018; Lallensack et al., 2015). Because photogrammetric digitization was not a primary aim during fieldwork, only three tracks were digitized. The maximum track length was measured according to the zone of “negative displacement” following Falkingham (2016). Photogrammetric models were produced from multiple digital photographs (camera model: OLYMPUS OM-D E-M5) which were converted into scaled, 3D textured mesh models using the software Agisoft Photoscan v1.4 (standard edition). The mesh models were then imported into the software Cloud Compare (www. couldcompare.org, version 2.9) where they were rendered with scaled false-colour topographic profiles. Our 3D models are available on figshare: https://doi.org/10.6084/m9.figshare.12753212

RESULTS

Tracks left by living animals

The bovid tracks are round in shape, with two distinctive thick hoofs (clear impression of the edge of the hoof; see arrows in Figure 5A–D) and possess a narrow medial ridge. Some tracks have the shape of an inverted V (Fig. 5A, B). They usually have a larger manus width than pes width. The anterior margin of the hooves is more pointed than the posterior edge. The anterior part of the impressions is generally much deeper than the posterior portion. The surfaces in Figure 5A–D are produced in moist clay.

The bear tracks are wider anteriorly and possess 5 forward pointing digit impressions (Fig. 5E–H). When tracks faithfully record foot morphology, as in our examples, the bear tracks lack a medial arch and possess digit impressions of sub-equal length. The bear tracks also have a digit I that is relatively longer than digit V, and display a distinctive fleshy metapodial pad. The manus claw impressions of the black bear (Ursus thibetanus) are sharper, shorter, and more curved than those of other bears that do not climb trees. The pes of the black bear shows the human-like configuration of a plantigrade or flat-footed posture (McDougall, 2015). The manus tracks of the black bear possess a large proximal palm, and the size of the fifth digit is larger than that of the first digit. Meanwhile, the pes tracks of the black bear retain their sole, and are more elongate compared to manus tracks (Fig. 5E–H).

For comparison with modern human tracks, we present images of two tracks made by humans on multi-layered palaeosurfaces (Fig. 5I, J). This study as well as others (e.g., Bennett and Morse, 2014; Roach et al., 2016) present examples of the morphological variability of human tracks left in different substrates. The infill is of a relatively small grain size, while the grain size of the surrounding surface is larger. These tracks may resemble those of bears. Should we not know the trackmaker, their elongation and weak medial arch would offer a small possibility that these were human tracks, so they might be confused with bear tracks. In fact, if substrate conditions are not ideal, unshod human tracks can record very little detail and appear as little more than elongated impressions, sometimes with a central constriction.

Tracks from Vértesszőlős

The trampled surface is on a calcareous mudstone, partly overlain by calcareous tuff. We re-describe three tracks previously studied by Kretzoi and Dobosi (1990). It is difficult to assess if these tracks are true tracks, because the palaeo-surface comprises several (partially thin) layers.

Track 1 (isolated impression)

This track was previously interpreted as being made by a small bear (Kretzoi and Dobosi, 1990). However, we find little similarity between this track (Fig. 6A–C) and those left by modern bears (Fig. 5E–H). The anterior part of the track has the shape of an inverted V, whereas the posterior part of the track has a rounded outline with a less evident V shape. Therefore, we interpret this morphology as being produced by two superimposed hoof tracks oriented towards the south of the site: a pes (Fig. 6B, blue) overstepping a manus (Fig. 6B, red), this is common in bovid tracks. This composite impression is the clearest of the three detailed here, possessing sharp edges and a mostly distinct outline.

Tracks 2 and 3 (associated impressions)

Two elongate impressions located in close proximity to each other (Fig. 6D and G, tracks 2 and 3) were previously identified as being made by bears (Kretzoi and Dobosi, 1990), but originally interpreted as hominin tracks (Vértes, 1964). If these impressions are truly tracks, then either they have been subjected to severe weathering/erosion, and are now poorly preserved, or they lacked anatomical fidelity when they were produced and are relatively well preserved as regards the post-formation processes (see Gatesy and Falkingham, 2017; Marchetti et al., 2019; Falkingham and Gatesy, 2020).

Topographically, the impressions cannot be objectively identified from the surrounding uneven surface (Fig. 6E). However, one of us (IT) visited the site and was able to differentiate between the base of the impressions and the surrounding surface based on texture. When the imprint and surrounding surface show different grain sizes, the infill is of a relatively small grain size, while the grain size of the surrounding surface is larger, suggesting that these may be modified true tracks, as opposed to undertracks (Fig. 6G). However, morphology does not allow to assess if these are single tracks or couples of two tracks, therefore, we refer to one track, which means either one track or one couple. On this basis, and in conjunction with the 3D model, outlines were produced of tracks 2 and 3 (Fig. 6E and H, respectively).

Superficially, the impressions resemble the general shape of unshod human tracks, with broader anterior ends and a narrower middle portion. The impressions are also of approximately the same size as a modern human track (~250 mm in length).
We find no evidence that the two impressions, if indeed they are tracks, form part of a trackway, and although both impressions are aligned in approximately the same orientation, this may be coincidental. Any mammal trackway comprising these two impressions would be unusually wide. We found no evidence of subsequent impressions that could be associated forming part of a longer trackway.

**DISCUSSION**

Of the three elongate impressions studied here (Fig. 5A, F, H), only one (Fig. 5A; Track 1) possesses enough morphological distinctiveness to be identified. Based on the sharp edges and central ridge, we interpret this track as being made by the superimposed manus and pes of a bovid, an interpretation which is supported by skeletal material found...
nearby (Kretzoi and Dobosi, 1990). The anterior hooves of the track are clear (Fig. 6A–C), therefore we assume the foot was parallel to the sediment during contact (Fig. 5B, D). Unfortunately, the highly irregular surface upon which the tracks are impressed precludes identification of any subsequent tracks constituting a trackway. Based on the shape of the central ridge, which is wider at the posterior margin in our extant bovid tracks (Fig. 5A–D), we interpret the trackmaker to have been moving toward the south of the site.

Tracks 2 and 3 are more problematic, and based on objective topography alone, one would be hard pressed to identify any specific impression. However, the infill is of a relatively small grain size, while the grain size of the surrounding surface is larger, suggesting that these may be modified true tracks. Superficially, they do resemble hominin tracks in both their general shape and size. Track 2 may have been a pes, because it seems to have a medial arc, while it is hard to assess whether track 3 is either a pes imprint or a manus-pes couple, because it is separated in two parts that may have had digit-like impressions. The distance between track 2 and track 3 (measure between top of both tracks) is about 70 cm. If track 3 is indeed a pes impression, the trackway width between track 2 and track 3 would be notably wide. Surrounding tracks do not reflect this, and therefore we do not know the relationship between track 2 and track 3. Previous studies have highlighted the morphological variability in tracks even from a single human trackmaker (Lockely et al., 2008; Marty et al., 2009; Morse et al., 2010; Wall-Scheffler et al., 2015; Marchetti et al., 2019) and it is quite conceivable that the studied impressions (tracks 2 and 3) were made by a hominin foot, given the general form, which is supported by the presence of tools and Homo heidelbergensis body fossils in nearby strata. If they are indeed hominin tracks, the global average foot-length/stature ratio of 15% (Mietto et al., 2003) would indicate that the trackmakers were approximately 1.65 m tall. This value falls in the range of height estimated for Homo heidelbergensis from skeletons, which is 1.57–1.75 m (male average = 1.75 m; female average = 1.57 m; Carretero et al., 2012). However, the tracks lack any distinctive morphological features that could conclusively say if they were produced by hominins and not bears.

CONCLUSION

We investigated three tracks in the Vértesszőlős quarry using 3D photogrammetry techniques. All three impressions have previously been attributed to an Ursine trackmaker or to hominin tracks. Our analysis does not support either of these hypotheses. Instead, we attribute one track (Track 1) to a bovine trackmaker produced through a superimposition of manus and pes impressions.

The other two tracks remain inconclusive. Both impressions lack sufficient morphological features to interpret the trackmaker identity. Early human tracks are rare in the fossil record, and it is possible that tracks of Homo heidelbergensis are present at Vértesszőlős, given the presence of Palaeolithic tools and Homo skeletal remains in the area. Despite lacking anatomical details, the putative traces do share similarity with some modern human tracks made in similar limestone-mudstone deposits. However, the attribution to a hominid trackmaker of any of the three analysed tracks at site III cannot be supported unless future excavations expose more diagnostic impressions.

Acknowledgements

We thank Balázs Bradák for helpful discussions, and Yoshiaki Okamura for providing pictures. We are grateful to the editors, Hendrik Klein and Lorenzo Marchetti for help, and special thanks to the reviewers: Lara Sciscio and Christian Meyer, for their thoughtful comments and suggestions. This work was financially supported by a grant from the Japan Society for the Promotion of Science awarded to IT (15J00351), IT (17J03543) and partly by a grant from the Japan Society for the Promotion of Science 1532.

REFERENCES

Bennet, M. R. & Morse, S., 2014. Human Footprints: Fossilised Locomotion? Springer, London, 216 pp.

Buchwitz, M. & Voigt, S., 2018. On the morphological variability of Ichnootherium tracks and evolution of locomotion in the sistergroup of amniotes. PeerJ, 6: e4346.

Buckley, L. G., McCrea, R. T. & Xing, L., 2018. First report of Ignotorniidae (Aves) from the Lower Cretaceous Gates Formation (Albian) of western Canada, with description of a new ichnospecies of Ignotornis, Ignotornis canadensis ichnos. nov. Cretaceous Research, 84: 209–222.

Carretero, J. M., Rodriguez, L., García-González, R., Arsuaga, J. L., Gómez-Olivencia, A., Lorenzo, C., Bonmati, A., Gracia, A., Martinez, I. & Quam, R., 2012. Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain). Journal of Human Evolution, 62: 242–255.

CloudCompare (version 2.9) [GPL software]. (2017). Retrieved from http://www.cloudcompare.org/

Dobosi, V., 2003. Changing environment – unchanged culture at Vértesszőlős, Hungary. In: Burdikiewicz, J. M. & Ronen, A. (eds), Lower Palaeolithic small tools in Europe and the Levant. British Archaeological Reports, Oxford, pp. 101–111.

Elbroch, M., 2003. Mammal Tracks & Sign: A Guide to North American Species. Stackpole Books, Pennsylvania, 792 pp.

Falkingham, P. L., 2012. Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. Palaeontologia Electronica, 15, 15.1.1T, 1–15.

Falkingham, P. L., 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. Journal of Zoology, 292: 222–228.

Falkingham, P. L., 2016. Applying Objective Methods to Subjective Track Outlines. In: Falkingham, P. L., Marty, D. & Richter, A. (eds), Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington, pp. 72–81.

Falkingham, P. L., Bates, K. T., Avanzini, M., Bennett, M., Bordy, E. M., Breithaupt, B. H., Castanera, D., Citton, P., Diaz–Martinez, I., Farlow, J. O., Fiorillo, A. R., Gatesy, S. M., Getty, P., Hatala, K. G., Hornung, J. J., Hyatt, J. A., Klein, H., Lallensack, J. N., Martin, A. J., Marty, D., Matthews, N. A., Meyer, C. A., Milán, J., Minter, N. J., Razzolini, N. L., Romilio, A., Salisbury, S. W., Sciscio, L., Tanaka, I., Wiseman, A. L. A., Xing, L. D. & Belvedere, M.,
2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology, 61: 469–480.

Falkingham, P. L., Bates, K. T. & Farlow, J. O., 2014. Historical photogrammetry: Bird’s Paluxy River Dinosaur chase sequence digitally reconstructed as it was prior to excavation 70 years ago. PLoS ONE, 9, 4: e93247.

Falkingham, P. L. & Gatesy, S. M., 2020. Discussion: Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al. Earth-Science Reviews, 208, 103320. doi:10.1016/j.earscirev.2020.103320

Gatesy, S. M. & Falkingham, P. L., 2017. Neither bones nor feet: track morphological variation and ‘preservation quality’. Journal of Vertebrate Paleontology, 37, 1: e13149289.

Gierliński, G. D., Niedźwiedzki, G., Lockley, M. G., Athanassiou, A., Fassoulas, C., Dubicka, Z., Boczarowskic, A. & Bennett, M. R., 2017. Possible hominin footprints from the late Miocene (c. 5.7 Ma) of Crete? Proceedings of the Geologists’ Association, 128: 697–710.

Haas, J., 2013. Geology of Hungary. Springer, Berlin, 268 pp.

Helm, C. W., Cawthra, H. C., Combrink, X., Helm, C. J. Z., Rust, R., Steer, W. & van den Heever, A., 2020. Pleistocene large reptile tracks and probable swim traces on South Africa’s Cape south coast. South African Journal of Science, 116: 6542.

Hennig, G. J., Grün, R., Brunmacker, K. & Pécsi, M., 1983. Th\(^{230}\)/U\(^{234}\) sowie ESR-Altersbestimmungen einiger Travertine in Ungarn. Eiszeitalter und Gegenwart, 33: 9–19.

Kele, S., Markó, A., Čsah, J., Shen, C., Wu, C. & Bernasconi, M. S., 2016. Dating and clumped isotope-based temperature of a paleo-jacuzzi (Vértesszőlős Early Man site, Hungary). In: 5th International Clumped Isotope Workshop, 6–9 January, St. Petersburg, Florida, USA. [Editors unknown]. p. 026. http://mng.rsmas.miami.edu/groups/sil/abstracts/pdf

Klein, H. & Lucas, S. G., 2015. Evolution of the semi-aquatic lifestyle in archosaurs – evidence from the tetrapod footprint record. In: McIlroy, D. (ed.), Papers from ICHNIA III. Geological Association of Canada, Miscellaneous Publication, 9: 105–113.

Koenigswald, W. & Heinrich, W. D., 2007. Biostratigraphische Begriffe aus der Säugetierpaläontologie für das Plioizän und Pleistoizän Deutschlands. Eiszeitalter und Gegenwart, 56: 96–115.

Kretzoi, M. & Dobosi, V., 1990. Vértesszőlős – Man, Site, Culture. Akadémiai Kiadó, Budapest, 554 pp.

Kretzoi, M. & Vértes, L., 1965. The role of vertebrate fauna and Palaeolithic industries of Hungary in Quaternary stratigraphy and chronology. Acta Geologica Hungarica, 9: 125–144.

Lallensack, J. N., Sander, P. M., Knötschke, N. & Wings, O., 2015. Dinosaur tracks from the Langenberg Quarry (Late Jurassic, Germany) reconstructed with historical photogrammetry: Evidence for large theropods soon after insular dwarfism. Palaeontologia Electronica, 18, 2: 1–34.

Laudoux, L. & Boudade-Maligne, M., 2015. The contribution of geometric morphometric analysis to prehistoric ichnology: the example of large canid tracks and their implication for the debate concerning wolf domestication. Journal of Archaeological Science, 61: 25–35.

Lockley, M. G., Roberts, G. & Kim, J.-Y., 2008. In the footprints of our ancestors: an overview of the hominid track record. Ichnos, 15: 106–125.

Lucas, G. L. & Hunt, A., 2007. Ichnotaxonomy of camel footprints. In: Lucas, G. S., Spielmann, J. A. & Lockley, M. G. (eds), Cenozoic vertebrate tracks and traces. New Mexico Museum of Natural History & Science, 42: 155–168.

Mallison, H. & Wings, O., 2014. Photogrammetry in paleontology: a practical guide. Journal of Vertebrate Paleontology Techniques, 12: 1–31.

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing., L., Feola, S., Melchor, R. N., 2020. Reply to discussion of “Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present” by Marchetti et al. (2019). Earth-Science Reviews, 208: 103319.

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing., L., Feola, S., Melchor, R. N. & Farlow, J. O., 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. Earth-Science Reviews, 193: 109–145.

Marty, D., Strasser, A. & Meyer, C. A., 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. Ichnos, 16: 127–142.

McDougall, L., 2015. The Tracker’s Handbook: How to Identify and Trail any Animal, Anywhere. Skyhorse Publishing, New York, 368 pp.

Mietto, P., Avanzini, M. & Rolandi, G., 2003. Palaeontology: Human footprints in Pleistocene volcanic ash. Nature, 422: 133.

Morse, S. A., Bennett, M. R., Gonzalez, S. & Huddart, D., 2010. Techniques for verifying human footprints: reappraisal of pre-Clovis footprints in central Mexico. Quaternary Science Reviews, 29: 2571–2578.

Rouch, N. T., Hatala, K. G., Ostrofsky, K. R., Villmoare, B., Reeves, J. S., Du, A. B. D. R., Harris, J. W. K., Behrensmeier, A. K. & Richmond, B. G., 2016. Pleistocene footprints show intensive use of lake margin habitats by Homo erectus groups. Scientific Reports, 6: 26374.

Stringer, C., 2012. The status of Homo heidelbergensis (Schouens sack 1908). Evolutionary Anthropology, 21: 101–107.

Vértes, L., 1964. Az őskőkor és az átmeneti kor emlékei Magyarországon [Remains of the Paleolithic in Hungary]. Akadémiai Kiadó, Budapest, 385 pp. [In Hungarian.]

Wall-Scheffler, C. M., Wagner, J. & Wagler, E., 2015. Human footprint variation while performing load bearing tasks. PLoS ONE, 10, 3: e0118619.
