Revisiting the peroneal trochlea of the StW 352 calcaneus

AUTHORS:
Ellison J. McNutt[1,2] (iD)
Alexander G. Claxton[3] (iD)
Kristian J. Carlson[4,5] (iD)

AFFILIATIONS:
[1]Department of Anthropology, Dartmouth College, Hanover, New Hampshire, USA

[2]Ecology, Evolution, Ecosystems and Society, Dartmouth College, Hanover, New Hampshire, USA

[3]Department of Anthropology, Boston University, Boston, Massachusetts, USA

[4]Department of Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, USA

[5]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

CORRESPONDENCE TO:
Ellison McNutt

EMAIL:
Ellison.J.McNutt.GR@
Dartmouth.edu

StW 352, from Sterkfontein Member 4 (South Africa), is a partial calcaneus attributed to *Australopithecus africanus* and is dated to ~2.0–2.6 Ma. The unusual robusticity of the peroneal trochlea (PT) of StW 352 has been commented on by several authors. The size of hominin PTs has been hypothesised to be positively correlated with the degree of recruitment of peroneus longus during bipedal locomotion and/or climbing. Given the potential functional relevance of an enlarged PT for reconstructing hominin activity patterns, we present the following previously unrecognised structural details of the reconstructed StW 352 that affect current interpretations of its functional morphology: (1) we estimate that the PT has been reattached to the body of the calcaneus ~5 mm dorso-distally from its original anatomical position; and (2) the presence of intrusive matrix has artificially misshaped the PT by expanding it laterally and proximodistally. Future studies of this specimen that apply geometric morphometrics, or other shape analysis tools, should compensate for these inaccuracies before undertaking comparisons between it and other calcanei. Additionally, given that the PT is likely smaller than previously reported for StW 352, caution should be exercised when using it to infer muscle function and extrapolate activity patterns of this individual, and thus by extension, within *Australopithecus africanus* in general. Lastly, these findings highlight the importance of not only the production of accurate reconstructions, but also the critical evaluation of the accuracy of existing reconstructions when working with damaged fossil material.

Significance

- This work epitomises the value of critically evaluating original fossil reconstructions, especially of postcranial elements.

- New technologies (e.g. microCT) offer non-destructive opportunities for evaluating/improving the accuracy of fossil reconstructions.

- Re-assessing StW 352 suggests peroneal muscles may have factored less prominently in *A. africanus* locomotion than previously thought.

StW 352 is a partial right calcaneus from Member 4 of the Sterkfontein Cave formation, South Africa[1,2] dated to approximately 2.0–2.6 Ma.[3] Because of its provenience in Member 4, StW 352 has typically been attributed to *Australopithecus africanus*[4-6], but that assignation is potentially complicated by a lack of consensus on the number of australopith species present in Sterkfontein Member 4[7-9].

The distal end of StW 352 is generally well preserved with the exception of damage to the plantar half of the articulation with the cuboid and a missing posterior tubercle. The latter is completely sheared off proximal to the posterior talar facet. There are two additional major breaks running through the calcaneal body, but both have been repaired with an unidentified type of glue. The first of these runs in a parasagittal plane and completely separates the peroneal trochlea from the rest of the calcaneal body. The second is approximately coronal in orientation, passing proximal to the sustentaculum tali, but distal to the posterior talar facet (see Figure 1). Given that the second break does not bisect the peroneal trochlea, it is likely that the trochlea was sheared off prior to the second break.

One prominent feature of the *A. africanus* StW 352 calcaneus is the unusual robusticity of its peroneal trochlea, as has been noted by several authors.[2,5,10,11] This robusticity is noteworthy because apes tend to exhibit larger peroneal trochleae than modern humans[12], and the peroneal trochlea of an *A. afarensis* calcaneus also has been described as 'massive'[13]. The peroneal trochlea is responsible for redirecting the tendons of peroneus longus and peroneus brevis travelling distally from the leg to their insertion in the foot.[14] The peroneal trochlea acts as the anchor point for the retinacula surrounding the tendons of these peroneal muscles and, thus, its size has been hypothesised to vary with their size and activity.[15]

Stern and Susman[16] used telemetered electromyographic studies of peroneus longus and peroneus brevis activation in *Pan troglodytes* and *Homo sapiens* to suggest that a large peroneal trochlea could have implications for understanding their functional role during bipedal locomotion and/or climbing in *Australopithecus*. They noted that both peroneal muscles were active during the second half of stance phase in humans, likely used to maintain the forefoot in relative eversion and assist in 'locking' the metatarsal joints while transferring weight medially towards the big toe.[16] In *P. troglodytes*, by contrast, neither peroneal muscle was active during terrestrial quadrupedalism and both seemed to be only variably active during stance phase of bipedalism.[16] More recent electromyographic studies of these peroneal muscles have observed activity in chimpanzees similar to that in humans during the last half of stance phase of bipedal gaits.[17] By comparison, both peroneal muscles were very active in chimpanzees during stance phase of quadrupedalism on vertical and horizontal simulated arboreal substrates, likely to aid in everting the foot on such supports.[16] Stern and Susman[16] hypothesised that the large (ape-like) peroneal trochlea in *A. afarensis* corresponded to large peroneal muscles reflective of a foot being used in an arboreal setting.[16]
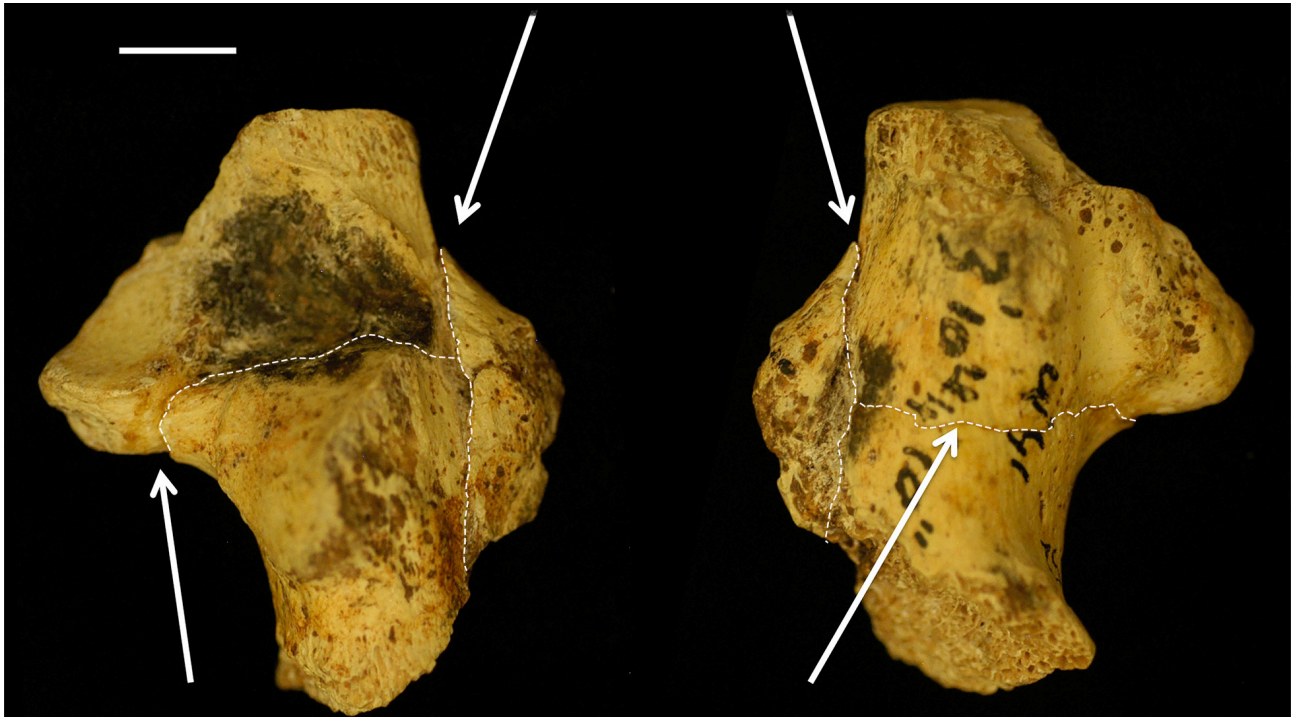
Figure 1: (Left) Dorsal and (right) plantar views of StW 352. Arrows and dashed lines highlight repaired breaks through the body of the calcaneus and separating the peroneal trochlea from the rest of the calcaneus. Note the lack of continuation of the 'horizontal' break through its intersection with the 'vertical' break in the illustration.

There are disagreements, however, about the degree to which arboreality was practised by *Australopithecus*.[13,18-21] If the size of the peroneal trochlea is correlated to frequent forceful contraction of the peroneal muscles, as has been suggested,[5,10,16] its position, size, and form informs in this debate. Given the uniqueness of the enlarged peroneal trochlea on StW 352, and thus its potential relevance for hominin functional morphology, we chose to carefully investigate its structural integrity using high-resolution computed tomography (CT).

Here, we critically evaluate StW 352's structural integrity, noting two issues that would affect current interpretations of the functional morphology of the reconstructed fossil. First, careful visual examination of the external surface of the peroneal trochlea suggests its proximodistal position may be incorrect. Upon close inspection, it appears that the peroneal trochlea has been reattached to the body of the calcaneus in such a way that there is cortical bone overlapping at both the dorsal and distal sides, leaving an artificial void inferior to the peroneal trochlea (see A and B in Figure 2). This malalignment suggests that the true attachment site should be more plantarly and proximally positioned compared to its current position. Second, the central region of the peroneal trochlea shows evidence of having been split and outwardly expanded by matrix infill, which appears to have spuriously augmented the overall robusticity of this anatomy, and its proximodistal dimension in particular (see C and D in Figure 2).

It is not uncommon to find evidence of taphonomic changes to the remains of fossil hominins from Sterkfontein Member 4. Multiple cranial and postcranial specimens from Sterkfontein Member 4 exhibit varying degrees of damage.[22-24] For example, many specimens show evidence of carnivore modification (i.e. bite marks), highlighting the important role of carnivores as accumulation agents in these deposits.[22] Thus, our suggestion of taphonomic or post-depositional modifications of StW 352 is not unusual for a specimen from Sterkfontein Member 4.

Visual examinations of external surfaces of the fossil were evaluated further using high-resolution CT. Because the objective here was to qualitatively examine structural integrity, specifically whether the trabecular struts and cortical shell within the fossil were correctly realigned, we compared similar high-resolution CT images from two representative extant hominoid calcanei. The comparative sample included an individual adult right calcaneus from a modern human (*H. sapiens*) and a chimpanzee (*P. troglodytes*), loaned from the Anthropology Department at Boston University and the Harvard Museum of Comparative Zoology, respectively. A chimpanzee calcaneus was included because chimpanzees represent the closest-living relatives to modern humans and have a peroneal trochlea that forms from a separate ossification site, as may have occurred in hominins with a large peroneal trochlea.[15] Chimpanzees also exhibit a generally more robust postcranial skeleton than modern humans, who appear to exhibit systemically lower bone mass, particularly with age.[25] Thus, by including the chimpanzee calcaneus, any gross differences in cortical and trabecular bone distribution, particularly those related to potential internal partitioning of the peroneal trochlea from the calcaneal body, generated by differences in the development of this anatomy should be accounted for in the current evaluation.

Image data from StW 352 were acquired using the industrial high-resolution CT scanner at the Evolutionary Studies Institute of the University of the Witwatersrand (Johannesburg, South Africa). Image data from the two comparative calcanei were acquired using the industrial high-resolution CT scanner at Harvard University's Center for Nanoscale Systems (Cambridge, MA, USA). Scan parameters for all specimens are listed in Table 1. Renderings produced from each image data set were sectioned in two planes through the peroneal trochlea in order to visualise the internal organisation: in a coronal plane (A) near its distal edge and in a transverse plane (B) through the dorsal surface (Figure 3). StW 352 was sectioned in a third plane: transversely (C) through the middle of the peroneal trochlea (Figure 4). There is an unusual partition of cortical bone separating the internal cavity of the peroneal trochlea of StW 352 from the internal cavity of the calcaneal body that is absent in the comparative material (A and B in Figure 3), both of which instead exhibit a single continuous internal cavity filled with trabecular struts extending from the lateral region of the calcaneal body into the peroneal trochlea. Section C (Figure 4) highlights the presence of intrusive matrix causing artificial outward (lateral) and proximodistal expansion of StW 352's peroneal trochlea.
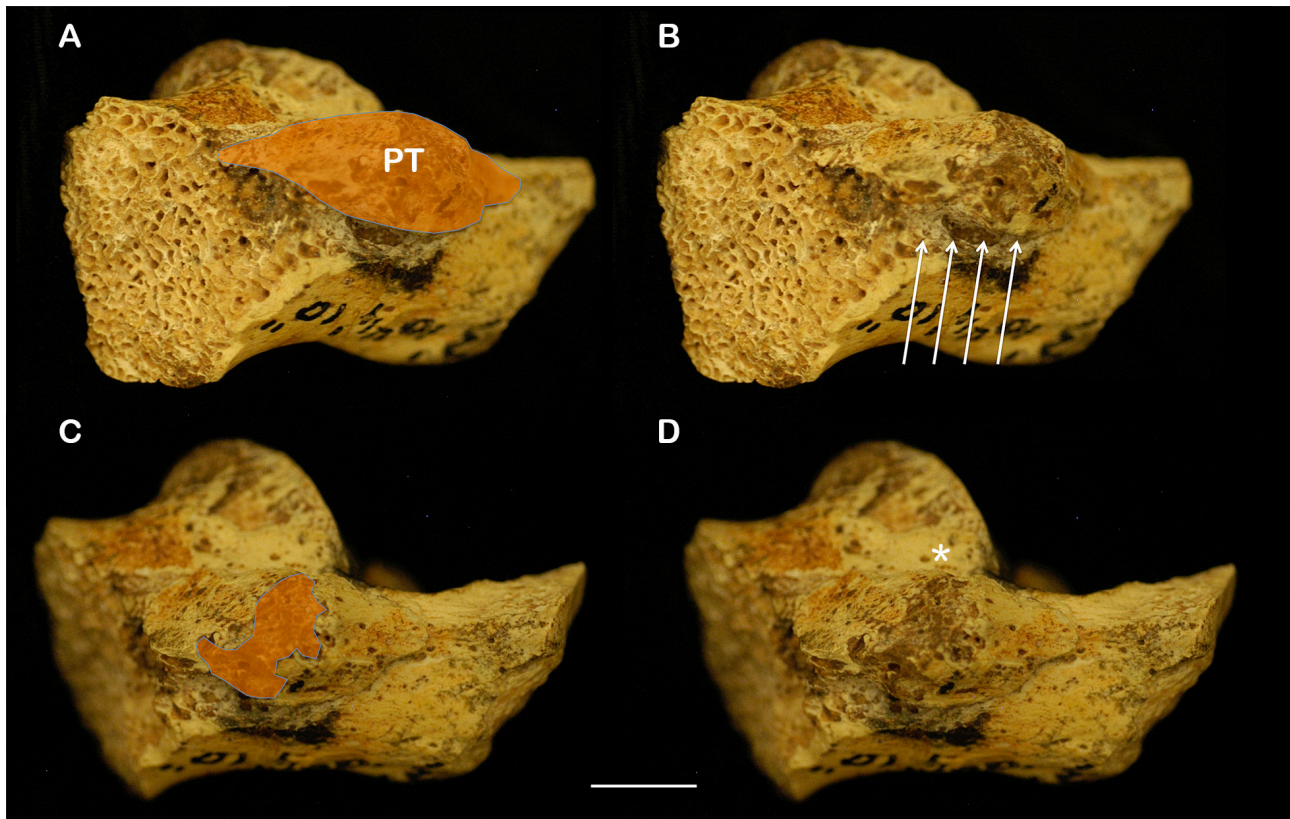
Figure 2: (A and B) Proximolateral views of StW 352. (A) Image highlighting the location of the peroneal trochlea (PT). (B) Arrows indicate the presence of a gap between the PT and the body of the calcaneus, which suggests that the true position of the PT should be more proximal and plantar than the current reconstructed position. (C and D) Lateral views of StW 352. (C) Highlighted outline of matrix infill. Notice how the proximal edge (to the left) may align fairly well with the dorsal edge (to the right), suggesting that these edges may refit if the intervening matrix was removed. (D) Unobstructed view of the splitting and expansion (underneath the star) of the middle of the PT caused by matrix.

Table 1: MicroCT scanning parameters for StW 352 and the comparative calcanei

Specimen number	Species	Scanning parameters				
		kV	µA	Voxel size (in μm)	Number of projections	Frames/second
BU 76	*Homo sapiens*	130	100	47.12	2958	1
MCZ 15312	*Pan troglodytes*	100	80	38.066	3092	1
StW 352†	*Australopithecus africanus*	90	135	29.6	5600	2

†Parameters taken from Zeininger et al.[6]

The high-resolution image data verify the initial visual examination of the external surface indicating that the peroneal trochlea in StW 352 has not been accurately reconstructed. Rather, it has been reattached to the main body of the calcaneus in an anatomically inaccurate position, and its robusticity (size and form) is at least partly enhanced by the remaining intrusive matrix. Its current form and the existing breakage pattern suggest that the peroneal trochlea must have been sheared away and proximodistally expanded before the coronally oriented break through the mid-body occurred. Some undefined period of time following this, the posterior tubercle appears to have been broken off and never recovered. Upon recovery of the existing fossil, the peroneal trochlea was reattached to the body approximately 5 mm dorso-distally (estimated from microCT image data) from its original anatomical position.

These observations have several implications. First, any future study of StW 352 employing geometric morphometrics, or other shape analysis tools, should compensate for the external displacement of its peroneal trochlea and use caution when commenting on the robusticity of its peroneal trochlea in comparative contexts. Moreover, a detailed digital reconstruction of the specimen would be advisable in order to more accurately reposition the peroneal trochlea and remove the excess matrix. Second, given the seemingly spurious outward expansion and proximodistal displacement observed, the actual size of the peroneal trochlea of StW 352 is likely smaller to an unknown extent and its anatomical position likely more proximal than previously described.[2,5,10,11] While correction of its size would lessen the robusticity of the peroneal trochlea to an uncertain precise extent, it would still appear to us to be relatively larger than typical human morphology. Nonetheless, because the size of hominin peroneal trochleae has been hypothesised to correspond with the degree of recruitment of the peroneal muscles,[5,16,18,26,27] and because this morphology is rarely preserved in the hominin fossil record, re-evaluation of StW 352 is crucial. Ultimately, we suggest that caution is warranted when using the present form of this bony anatomy on StW 352 to support interpretations of either an increased reliance on arboreal substrates or the peroneal muscles functioning as a possible compensatory mechanism for a less-developed medial arch during striding bipedalism in either this individual or, by extension, within *A. africanus* in general.
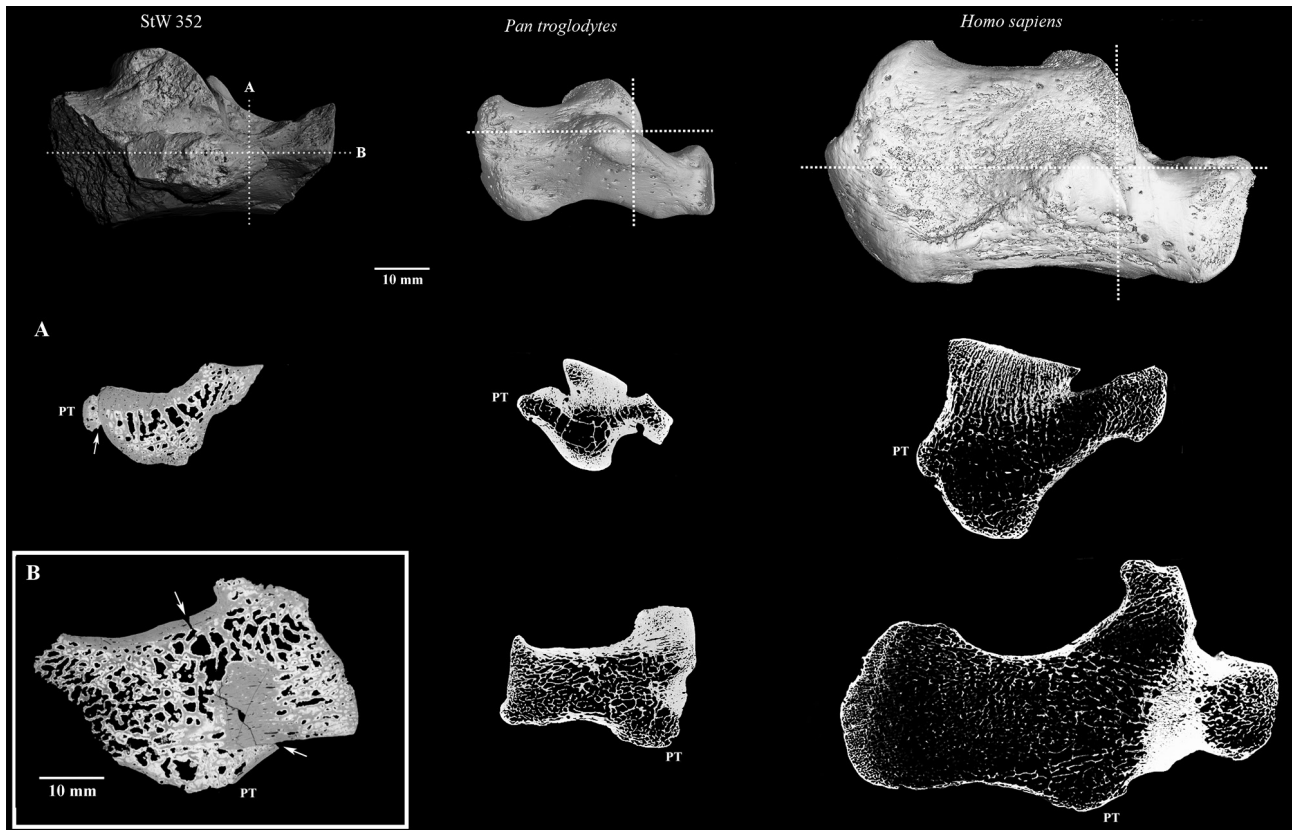
Figure 3: [From left to right] Top row: Lateral views of calcanei renderings from StW 352, *Pan troglodytes* and *Homo sapiens* showing the microCT sectional planes. Middle row: (A) Coronal section through the distal end of the peroneal trochlea (PT). Note the arrow indicating the presence of cortical bone under the PT of StW 352, but not in analogous locations in the comparative specimens. Bottom row: (B) Transverse section through the dorsal surface of the PT. Arrows indicate the location of both breaks through the body of StW 352 and the lack of similar cortical bone overlap in the comparative specimens.
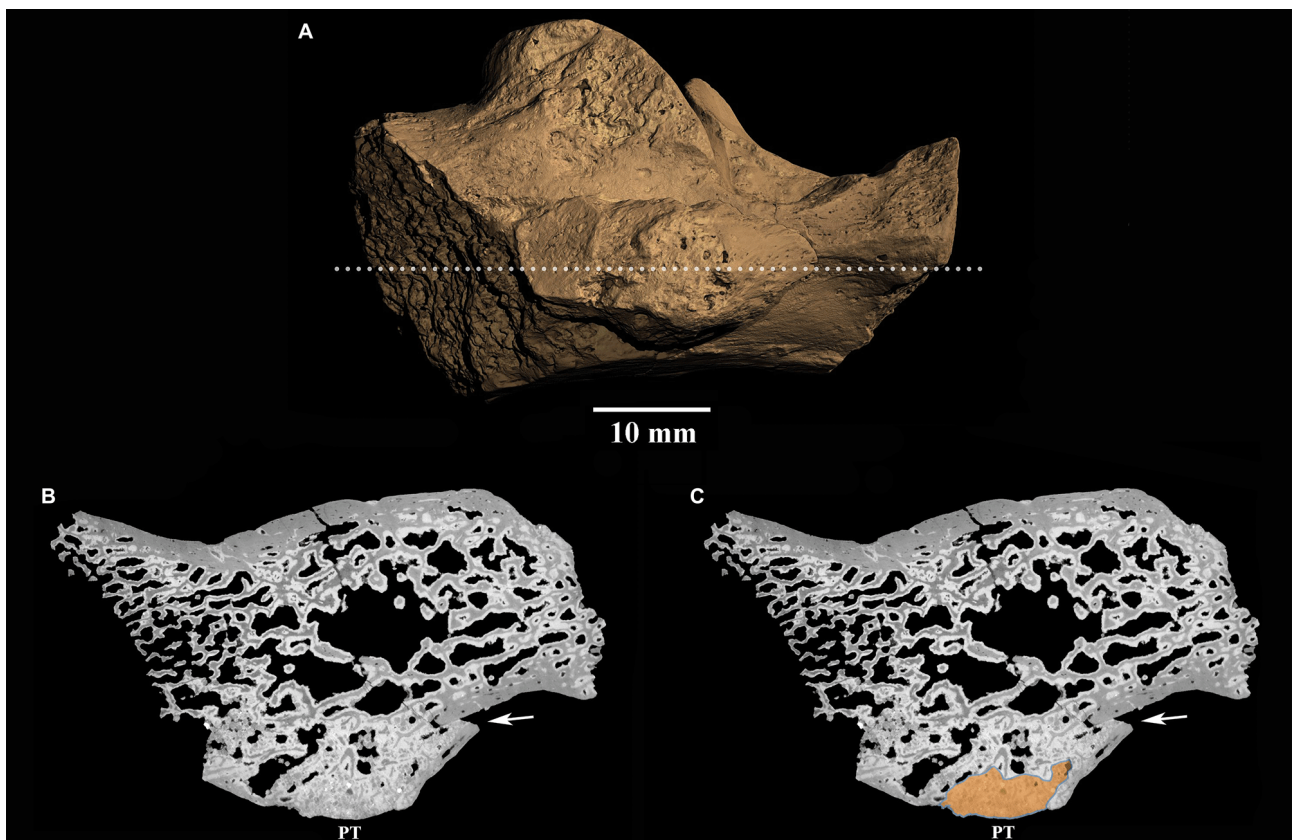

Figure 4: (A) Lateral view of StW 352 with the dotted line indicating the location of the transverse section through the middle of the peroneal trochlea (PT). (B) MicroCT image showing internal structure of the PT. Arrow indicates the area in which evidence of misalignment is best visualised. Note the presence of matrix infill located above the 'PT' label. (C) Repeat of image B with the shaded area demarking the approximate extent of the matrix infill.

Authors' contributions

The study was conceived by E.J.M. The paper was written by E.J.M. with contributions and revisions by K.J.C. and A.G.C. Project design and data collection were completed by E.J.M., K.J.C. and A.G.C.

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