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A Late Pleistocene Human Pedal Phalanx From the Pinnacle Point PP5-6N Rock-Shelter, Western Cape Province, South Africa

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ABSTRACT

Objectives: This study provides the description and comparative morphometric analysis of a non-hallucial distal pedal phalanx (PP 654270) excavated from near the base of the LBSR Stratigraphic Aggregate in the Pinnacle Point PP5-6N rock-shelter. It derives from a thin combustion feature (probably an in situ hearth) at the contact of two major stratigraphic aggregates, the transition of which has a modeled age range of 91.9–86.0 ka, which places this fossil in MIS 5b.

Material and Method: This phalanx (PP 654270) is assessed as representing a distal phalanx probably from the right side of Ray II or III. This bone adds to the very meager sample of pedal phalanges from the late Pleistocene of southern Africa. We compared the metric variables of this phalanx to several fossil and recent *Homo* samples.

Results: The bone has a comparatively thin cortex and a diffuse trabecular network in the proximal and especially the distal ends. The phalanx is long, narrow, and relatively gracile in comparison to Neandertal homologues.

Discussion: The phalanx PP 654270 displays similarities with penecontemporaneous Eurasian Middle Paleolithic and recent modern humans, although it tends to be comparatively long for Ray II and III homologues in these samples.

1 | Introduction

Southern African Middle Stone Age (MSA) sites that date to Marine Isotope Stages (MIS) 6–3 have featured prominently in discussions about the emergence of modern human behavior and morphology. In large measure, they have been emphasized because of the archeological debris they preserve (e.g., Conard 2008; Deacon 2001; Klein 2001; Lombard 2021; Marean 2015; Marean et al. 2007; Mitchell 2024; Sealy 2016; Wadley 2015; Wurz 2008). A total of 15 sites within this temporal span preserve human remains, but with few exceptions these mostly take the form of isolated teeth and small cranial and/or postcranial fragments (Table 1) (Grine 2016; Grine, Marean, et al. 2017; Grine et al. 2020). Eleven of these sites are situated along the coastal margin of South Africa, with Border Cave, Witkrans, Plovers Lake and Hofmeyr located inland. Klasies River Main Site is by far the richest, with nearly 50 human fossils spread across three stratigraphic members that span some 40,000 years (Grine et al. 2020; Grine, Wurz, and Marean 2017). Die Kelders Cave 1 is the second richest site, having yielded 28 specimens (Grine 2000; Grine, Marean, et al. 2017). In view of the relative paucity of human remains from the MSA of Southern and, Indeed, sub-Saharan Africa (Grine 2016), every discovery is worthy of documentation. We here report on an additional human specimen—a pedal distal phalanx—from the MSA deposits of Pinnacle Point (PP) 5-6 North (PP5-6N).

1.1 | Background to PP

PP is a rocky headland on the Indian Ocean coast near the town of Mossel Bay preserving an abundance of caves and rock-shelters (Figure 1A). Since 1999, PP has been under study by a transdisciplinary scientific team (the South African Coast Paleoclimate, Paleoenvironment, Paleoecology, Paleoanthropology Project, or SACP4), and it was declared a UNESCO World Heritage Site in 2024 in recognition of the important archeological records it preserves. The caves and rock-shelters are sea-cut features in Table Mountain Sandstone Formation quartzite (Karkanas et al. 2015, 2020) (Figure 1B,C) that are generally overlain by calcrete that provided alkaline buffering from what normally would have been acidic conditions (Bar-Matthews et al. 2010), thus providing for well-preserved faunal remains in most instances. The caves and rock-shelters were initially cut by sea levels at some ~1.1 Ma (Pickering et al. 2013) (Figure 1D), and the peak Marine Isotope Stage (MIS) 11 high sea stand at ~400 ka, which was at about +13 m above mean sea level (AMSL) in this area (Roberts et al. 2012). Sea stands of MIS 11 and MIS 5e, which were at about +5–6-m AMSL in this area, would have washed out most of the > 130 ka sediments from the caves, although some of these are sporadically preserved (Karkanas et al. 2020; Marean et al. 2007).

The hominin phalanx was excavated from the PP5-6 north (PP5-6N) rock-shelter. PP5-6 south (PP5-6S) is a cave to the southwest of PP5-6N, and at one time they were connected by sediments which are now mostly eroded away. Among the numerous sites at PP, PP5-6 and PP13B have received the most intense excavation and study. Together, they provide an archeological sequence from ~162 to 50 ka, and include the only archeological sediments confidently dated to MIS6 on the South African coast (Jacobs 2010; Jacobs et al. 2025; Marean et al. 2010; Smith et al. 2018). PP13B dates from about 162–90 ka, at which time it was sealed by a dune (Jacobs 2010; Marean et al. 2010). PP5-6 is dated using 169 optically stimulated luminescence ages, along with the Toba cryptotephra (Smith et al. 2018), input into a Bayesian age model (Jacobs et al. 2025). In this paper, all PP5-6 age estimates derive from the new Bayesian model (using 95.4% probabilities) and the Toba isochron. Human occupation dates from ~110 to 50 ka, at which time sediments in the rock shelter of PP5-6N appear to have nearly filled the site to the ceiling, making it unattractive for occupation.

TABLE 1 | Southern African hominin-bearing sites dating from MIS 6 through MIS 3.

Within MIS	Site	Age (ka)	Human remains
6–3	Border Cave	170–56	Jaw, humerus, ulna, two metatarsals?
6–5c	Pinnacle Point	162–50	Parietal; tooth; pedal distal phalanx
5e	Blind River	124–112	Femur
5e–4	Klasies River	115–58	Many teeth, cranial and postcranial fragments; two manual distal phalanges
5e–5a	Sea Harvest	110–71	Manual distal phalanx; tooth
5c–3	Ysterfontein 1	103–50	Three teeth
5c–3	Equus Cave	103–30	Eight teeth
5c–5a	Blombos	102–70	Nine teeth
5c–3	Witkrans	100–50	Three teeth
5a–4	Plovers Lake	89–62	Postcranial fragments
4	Die Kelders	74–59	Twenty-four teeth; mandibular fragment; three manual distal phalanges
4	Klipdrift Shelter	72–52	Isolated tooth
3	Sibudu	77–38	Manual distal phalanx; "toe bone?"; distal fibula; sternum; teeth
3	Diepkloof Shelter	61–48	Two pedal phalanges (intermediate & distal 5th ray); tooth
3	Hofmeyr	36	Cranium and mandibular fragment

Note: The age ranges provided for a site are the maximum and minimum estimates for the site and do not include the confidence intervals for individual sample averages. References relating to the hominin fossils from these sites can be found in Grine (2016), with additional citations for Sibudu (Will et al. 2019), Klasies River Main Site (Grine et al. 2020) and Die Kelders Cave 1 (Grine, Wurz, and Marean 2017).

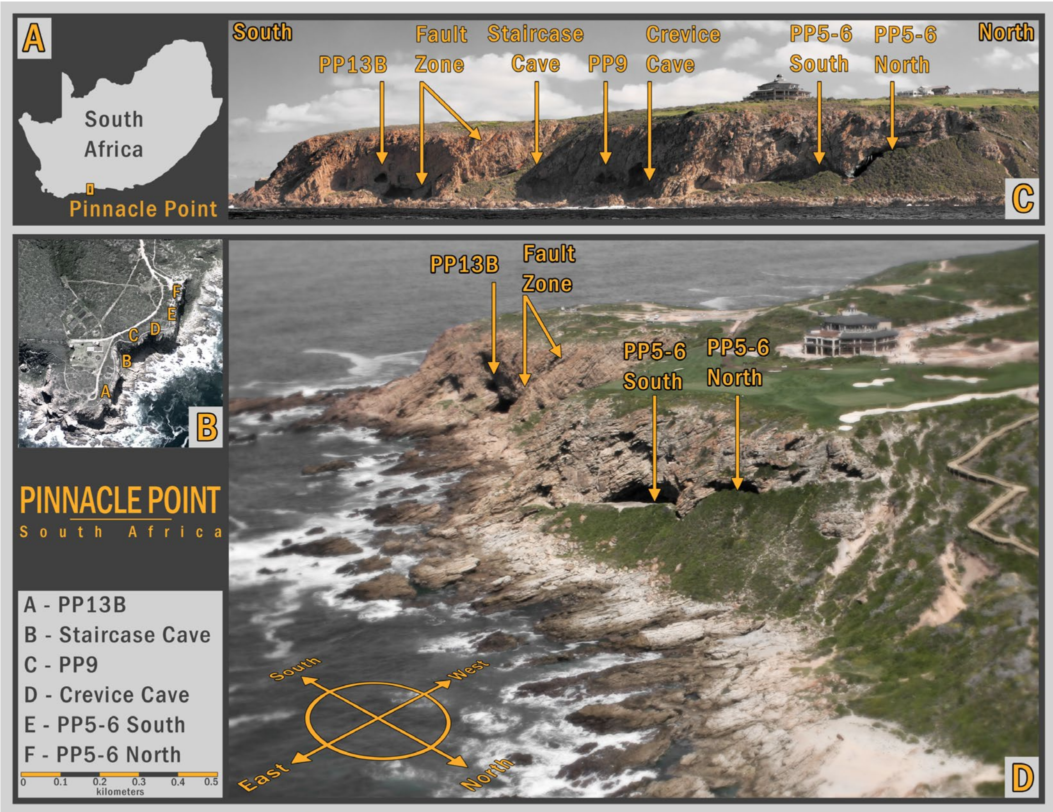

FIGURE 1 | The location and the major sites and features at Pinnacle Point. (A) Location of Pinnacle Point in South Africa. (B) Aerial view of the cliffs and the locations of the major caves and rock-shelters. (C) View of Pinnacle Point from the sea. (D) Pinnacle Point caves and rock-shelters viewed from the Northeast. Image by Erich Fisher.

Today the sea is within tens of meters of the sites, but through most of the occupation, sea levels were lower, and the coast was at most some 20 km further away (Fisher et al. 2010), although there is almost continuous exploitation and discard of mollusk remains in the sites. PP13B documents the earliest systematic use of mollusks, and very early worked ochre back to ~162 ka (Jacobs 2010; Marean et al. 2007). By ~110 ka, a true coastal adaptation is documented where shell middens are present and cultural artifacts such as seashells document a life embedded in the sea and its resources (Jerardino and Marean 2010; Marean 2010, 2011). The sequence at PP13B shows its most intense occupations when the coast is closer than 5 km to the site, with occupation intensity dropping off when the coast is further away. Hunting of large mammals is well documented throughout the sequence (Rector and Reed 2010; Thompson 2010).

Stone tools are dominated by a conventional MSA technology made primarily on quartzite throughout the sequence at PP13B (Thompson et al. 2010; Wilkins et al. 2017). The earliest evidence for stone tool heat treatment is present on silcrete dating back to about 162 ka (Brown et al. 2009; Jacobs 2010), and while present in small amounts throughout the sequences, it shows a sharp increase in abundance ~74 ka in PP5-6N. Very early microlithic technology appears at PP5-6N at ~74.0–72.7 ka (Brown et al. 2012; Jacobs et al. 2025), after deposition of the Toba cryptotephra (Smith et al. 2018). Subsequently, small bladelet technology is evidenced on a variety of raw materials alongside the more conventional quartzite-dominated MSA.

1.2 | Context of the PP Hominin Specimens

The phalanx was excavated and individually plotted (Plotted Find #654270) on March 2, 2017. Total station measurements of −3,786,847.52 (southing), −83,727.18 (westing), 15.50 AMSL were recorded (Hartebeesthoek94 Datum). One of us (K.E.) recognized it as unusual and probably primate while cataloging the excavated finds in January 2020; it was subsequently confirmed as hominin in 2024 by F.E.G. and N.C. It derives from Stratigraphic Unit LS17T1NV within Stratigraphic Sub-Aggregate Tove Red within Stratigraphic Aggregate Light Brown Sand and Roofspall (LBSR) at the very base contacting the underlying Yellow Brown Sand and Roofspall (YBSR). The transition from the YBSR to the LBSR is modeled at 91.9–86.0 ka, which represents an excellent age range for this specimen given its location at the contact of the YBSR and LBSR. Descriptions of the stratigraphy and nomenclature can be found in Karkanas et al. (2015) and Jacobs et al. (2025).

Stratigraphic Unit LS17T1NV is a thin combustion feature (probably an in situ hearth). The toe bone is dark brown (DB)/black in color, which is consistent with its context. There are 231 other plotted finds from this unit, including lithics, mollusks, mammalian fauna, fire cracked rock, and small bits of charcoal.

Two other hominin fragments, comprising a parietal fragment and an isolated permanent molar, were found at PP13B (Marean et al. 2004). Both were found out of context in loose sediment that resulted from shallow digging by members of the general public. The disturbance had occurred shortly before the first excavations in 2000, and it was interpreted as resulting from shallow shoveling to level sediment for a tent. That shoveling cut into an MSA layer described as the Brown Sand MSA Facies in the report on the test excavations (Marean et al. 2004). Further excavations refined the understanding of the Brown Sand MSA Facies, where it was renamed the Dark Brown Sand. The two hominin specimens were regarded as probably coming from DB Sand 2, which is dated between 102 and 91 ka (Jacobs et al. 2011; Marean et al. 2010).

Although it is impossible to identify exactly the sediments from which the two hominin specimens derive, it can be stated with reasonable confidence that they do not derive from layers significantly older than DB Sand 2, because these layers were not exposed to the surface. In addition, the fossils must predate 90 ka, because the cave was sealed by a dune at ~90 ka (Jacobs et al. 2011; Marean et al. 2007), as revealed from studies of intercalated and dated speleothem and sand from PP13B and other associated caves (Bar-Matthews et al. 2010). Indeed, the back slope of the dune that would have covered the entire portion of the western PP cliff face is preserved on the cave wall at PP13B.

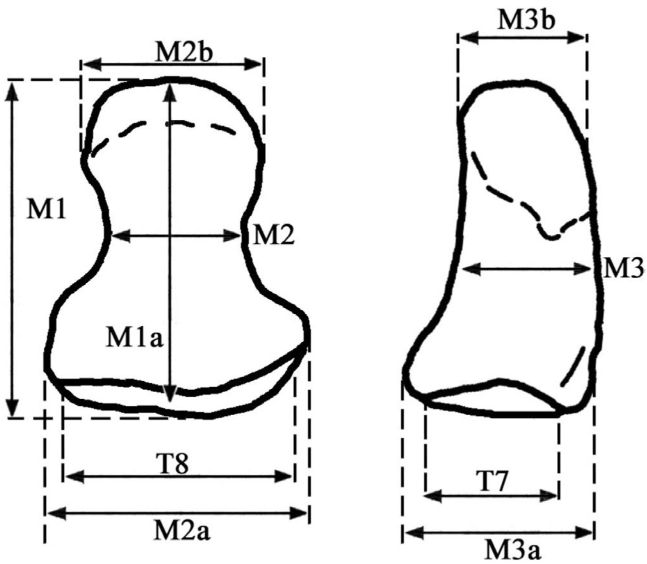

FIGURE 2 | Measurements recorded for the distal pedal phalanx from Pinnacle Point. Views: left = dorsal, right = medial. Abbreviations: M1, maximum length; M1a, articular length; M2, mid-diaphyseal breadth; M2a, proximal breadth; M2b, distal breadth; M3, mid-diaphyseal height; M3a, proximal height; M3b, distal height; T7, proximal articular height; T8, proximal articular breadth.

2 | Materials and Methods

2.1 | Nano-CT Scanning

The phalanx was examined by nano-computed tomography (General Electric Nanotom S) at Stellenbosch University at an accelerating voltage of 60 kV and at a voxel size of 0.01413 mm in the x, y and z axes. X-ray projection images were acquired in 2200 steps during a full rotation of the sample. At each step position, the first image was disregarded, and the subsequent two images averaged to produce higher quality images than standard. A detector shift was activated to minimize ring artifacts. The images utilized here were rendered in Volume Graphics VGStudio Max 3.0.

2.2 | Variables Measured

Ten linear measurements of the bone were recorded with calipers and confirmed using surfaces rendered from the nano-CT scans in Avizo v9.2.0. The osteometric variables employed here are the standard linear measurements that have been applied in other studies of pedal phalanges (Figure 2). These variables are largely congruent with those defined by the Martin system (Bräuer 1988); but see Trinkaus and Patel (2016) and Pablos, Gómez-Olivencia, Maureille, et al. (2019). The metrical variables were selected to describe the general morphology and articular size of the PP 654270 phalanx. As a measure of robusticity we used the robusticity index, which is defined as the average of the two diaphyseal diameters (M2 and M3) divided by the articular length (M1).

2.3 | Comparative Samples

Three samples of Late Pleistocene *Homo* phalanges (Neandertals, Middle Paleolithic modern humans (MPMH) and Upper Paleolithic (UP) humans) as well as three samples of recent/Holocene human phalanges were employed in the metrical and morphological comparisons of PP 654270.

Unfortunately, it is not always possible to determine precisely the ray from which a non-hallucial distal pedal phalanx derives unless the foot bones are in direct association (Carretero et al. 2015; Pablos, Gómez-Olivencia, Maureille, et al. 2019; Trinkaus 2016). This is especially true in the fossil and archeological record, where isolated elements may be taphonomically degraded. It is, however, commonly possible to discern distal phalanges from Rays II and III versus those that belonged to Rays IV and V. As noted below (see Section 3.1), we regard PP 654270 as most likely having derived from the second or third ray owing to the very slight medial deviation of the distal tuberosity. Although we cannot rule out the possibility that it belonged to a fourth or even the fifth digit, we have focused our comparisons with those elements that have been identified as belonging to Rays II and III. We provide supplemental comparisons with distal phalanges that have been identified as deriving from Ray IV and Ray V from these samples. There are a number of fossil distal phalanges from penecontemporaneous Middle Paleolithic and UP sites in Eurasia for which the lateral ray cannot be determined beyond a designation from II to V. These are listed in Table S1. They were excluded from the present analyses owing to the fact that such uncertainty in lateral ray identification will introduce unnecessary levels of uncertainty in statistical evaluations. In addition, and for the same reason, the *Homo naledi* sample of six distal pedal phalanges (Harcourt-Smith et al. 2015) was excluded from comparison. Although this South African hominin sample is geographically proximate, it is likely to be considerably older than PP and the other comparative samples with estimates of between 335 and either ~241 or 236 ka, corresponding to MIS 9–7 (Dirks et al. 2017; Robbins et al. 2021).

Moreover, its phylogenetic relationships with *Homo sapiens* versus either *H. erectus* or even *H. habilis* are currently unresolved (Dembo et al. 2016), and the fossil sample from the Rising Star cave system comprises very small individuals, with estimated average stature of 139–148 cm (4.5–4.8 ft) and body mass of 33.1–43.4 kg (73–96 lbs) (Garvin et al. 2017). Also excluded from consideration here are the unassigned distal pedal phalanges from the geographically distant East Asian (Jinniushan 1; Pearson 2000) and Indonesian (LB 1/43 and LB 1/57 attributed to *H. floresiensis*; Jungers et al. 2009) fossils.

With regard to the fossil samples, all ray-assigned Neandertal and Late Pleistocene *H. sapiens* distal pedal phalanges were included in the analyses. Although we recognize that Neandertals are characterized by possessing comparatively robust and broad distal pedal phalanges with expansive apical tuberosities in relation to *H. sapiens* (Pablos, Gómez-Olivencia, and Arsuaga 2019; Pablos, Gómez-Olivencia, Maureille, et al. 2019; Pearson et al. 2020), we have included them to ensure that our comparisons are as comprehensive as possible. The Late Pleistocene sample comprised MPMH primarily from the MIS 5 fossils from Skhūl and Qafzeh (McCown and Keith 1939; Vandermeersch 1981). Although there are several distal manual phalanges known from penecontemporaneous South African MSA sites (Klasies River Main Site, Sea Harvest, Die Kelders and Sibudu), the only distal pedal phalanx available for comparison is the MIS 3 specimen from Diepkloof Rock Shelter (Table 1). This bone (DRS-2) has been identified as a fifth toe (Verna et al. 2013). It is included here as part of the MPMH sample.

Our UP sample is composed of modern humans from Western Eurasia. When the antimeres of the distal phalanges are preserved by the fossil individuals (e.g., Kiik-Koba 1, Mirón 1 and Qafzeh sample), we averaged the available bilateral measurements to provide a mean value for each individual in order to better represent the variability among individuals rather than elements.

In addition to the Pleistocene fossil samples, we have included data from three recent/late Holocene comparative samples. These are the Hamann–Todd Osteological Collection from 20th century North America (Cleveland Museum of Natural History; $n = 167$), the San Pablo Medieval collection (Universidad de Burgos; $n = 16$) and the Woodland Native American collection from the Libben site, Ohio (Kent State University; $n = 20$) (Trinkaus 1975; pers. comm.). The Libben sample serves to take into consideration the fact that the footwear use in recent populations might influence pedal morphology (Trinkaus 2005). All three recent modern human samples are pooled sex samples.

Although all four lateral pedal rays are included in these samples, we have focused mainly on those distal phalanges identified as belonging to the second or third toe.

2.4 | Statistical Analysis

A comparative univariate analysis of all variables was conducted for the PP 654270 phalanx. In order to compare the individual values from this fossil with the averages from the different samples, the *Z*-scores were calculated when the comparative sample size was ≥ 4, and a value of 1.96 was considered significant ($p < 0.05$; Sokal and Rohlf 2003). For statistical analysis, we used STATISTICA 8.0 (Statsoft. Inc 2007).

3 | Results

3.1 | Description of the PP Pedal Phalanx

The specimen, cataloged as PP 654270, comprises a complete, well-preserved distal pedal phalanx (Figure 3). It is clearly not a hallucial phalanx. Its size and the relatively symmetrical waisting of its elongated shaft make it unlikely to derive from Ray V, although this possibility cannot be discounted completely. The proximal epiphysis is completely fused (Figure 4a,b), which is consistent with its derivation from an adult individual, as this occurs at ≥ 18 years in Rays II–V of recent females and males (Cardoso and Severino 2010). There is a slight degree of erosion to the medial side of the dorsal rim of the proximal epiphysis (Figure 4d). The bone is compressed in its dorsoplantar (DP) dimension (Figure 4c) and the proximal articular facet is slightly bi-concave. The distal tuberosity is slightly expanded relative to the width of the diaphysis, and it exhibits a very slight cant, which we interpret as being medially directed. The long axis of the element is virtually perpendicular to the transverse axis of the proximal facet. Viewed from its medial (or lateral) aspect, the plantar surface has a gently convex dorsal inflection from the proximal surface to the tip of the bone. The plantar surface has a moderately deep excavation surmounted distally by a flange-like enthesis for the insertion of the tendon of flexor digitorum longus. The nano-CT scans (Figure 4) reveal a moderately thick cortex in the region of the diaphyseal midshaft and across the proximal articular surface. The cortex thins somewhat over the distal end of the bone. The distal end and especially the proximal metaphysis possess moderately dense trabecular networks. Although the bone has a DB/black color and derives from what is interpreted as a combustion feature (stratigraphic unit LS17T1NV), there is no evidence either externally or internally of any shrinkage. We therefore regard the measurements of the specimen to accurately reflect its in vivo size. The bone lacks any evidence of either human- or carnivore-induced surface modification.

The bone's size and morphology correspond to a right distal lateral pedal phalanx. We regard PP 654270 as most likely having derived from the second or third ray owing to the very slight medial deviation of the distal tuberosity, although we cannot rule out the possibility that it belonged to a fourth or even the fifth digit.

With regard to the distal phalanges of the second to fifth toes, it is, as noted above, oftentimes difficult to assign either the side or especially the ray number unless they are found in articulation with the proximal and middle phalanges, or the distal phalanx is part of a complete or nearly complete series (Pablos, Gómez-Olivencia, Maureille, et al. 2019; Trinkaus 1983). Thus, the ray from which PP 654270 derived should be regarded as tentative. Moreover, isolated distal phalanges from the second and third rays are nearly indistinguishable (Pablos and Arsuaga 2024; Pablos, Gómez-Olivencia, and Arsuaga 2019; Trinkaus 2016).

FIGURE 3 | Volumetric renderings of the Pinnacle Point (PP 654270) distal pedal phalanx. Top row left to right: dorsal, plantar, lateral views; bottom row left to right: proximal, distal, medial views. Scale in mm.

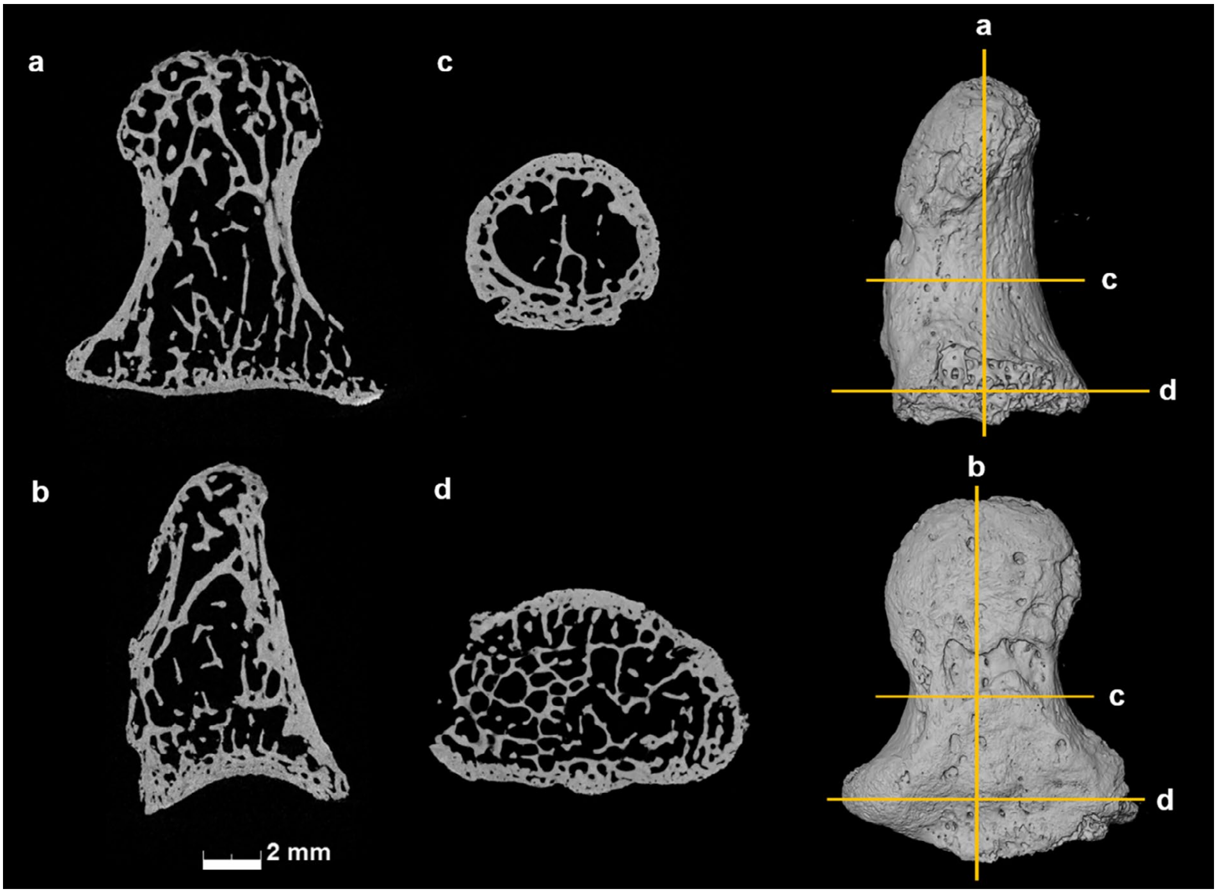

FIGURE 4 | Nano-CT slices through Pinnacle Point (PP 654270) distal pedal phalanx to show trabecular structure and distribution. (a) Horizontal section, (b) longitudinal section, (c) transverse section through diaphyseal midshaft, (d) transverse section through the mesial metaphysis.

Differentiating between Rays IV and V is based on size when they derive from a single foot (Carretero et al. 2015; Pablos, Gómez-Olivencia, and Arsuaga 2019; Pablos, Gómez-Olivencia, Maureille, et al. 2019; Trinkaus et al. 2014). Because PP 654270 is an isolated element, we have included all four lateral toes in our comparative samples of fossil and recent distal phalanges in order to ensure more complete analyses.

The values of the 10 osteometric variables recorded for PP 654270 and the descriptive statistical parameters of all the comparative samples for Rays II and III are recorded in Table 2. For a comparison with digits IV and V, see Table S2.

3.2 | Morphometric Comparisons

As noted above, a persistent difficulty in the study of isolated pedal lateral (second through fifth) phalanges is the attribution to the correct ray for comparisons. Identification of the fifth digit is often possible given the abbreviation of this toe in humans (Pablos and Arsuaga 2024; Pablos, Gómez-Olivencia, and Arsuaga 2019), but other three (second to fourth) cannot be reliably assigned to a digit unless multiple phalanges are preserved (e.g., Carretero et al. 2015; Pablos, Gómez-Olivencia, Maureille, et al. 2019; Trinkaus 1983). In such instances, ray attribution is mainly based on the decreasing lengths of the phalanges from II to IV. We reiterate that the assignment of PP 654270 to the second or third digit is therefore tentative. The small sample of reasonably securely identified distal phalanges from the Late Pleistocene precludes an in-depth analysis. Nevertheless, some interesting conclusions can be drawn from this study.

For nearly all variables, the PP phalanx values fall comfortably within the ranges of variation in Rays II and III of Neandertals as well as the various fossil and recent modern human samples. At the same time, however, PP 654270 differs from the comparative sample *averages* in some dimensions (Table 2). In general, PP 654270 is longer than the averages of toes II and III of all the samples except Neandertals. Unfortunately, small sample sizes preclude statistical assessment in many instances, but PP 654270 is significantly larger than Ray II of the MPMH for the maximum length (M1) and Rays II and III of the Libben Amerindian samples for articular length (M1a) (Figure 5A). The PP phalanx is narrower than that of Neandertals for toes II and III in all four breadth measurements (i.e., M2, M2a, M2b, and T8), but it differs significantly only in the width of the distal tubercle (measurement M2b) of Ray II (Figure 5B). In this dimension, PP 654270 is within the range of variation of the second and third phalanges of MPMH and UP samples. Unfortunately, the small sizes of these comparative fossil samples preclude any in-depth analyses.

The proximal articular breadth (measurement T8) of PP 654270 falls outside of the range of variation of all MPMH phalanges for Rays II and III. Here too, however, the small sample size of this comparative population precludes any exhaustive conclusion. The DP heights (measurements M3, M3a, M3b, and T7) of the PP phalanx do not differ significantly from the means of any of the comparative samples (Figure 5C). Nevertheless, PP 654270 falls below the range of variation of Rays II and III phalanges for some of the height dimensions of the Neandertal and MPMH samples. This seems to indicate that the PP phalanx may be comparatively shallow in its DP height in comparison to other modern human phalanges. Larger samples of phalanges are needed to confirm or refute this premise.

Neandertals and their ancestors possess higher levels of robusticity in their postcranial bones than do *H. sapiens* specimens (Arsuaga et al. 2015; Lorenzo et al. 2015; Pablos and Arsuaga 2024; Pablos et al. 2012; Trinkaus 1983; Trinkaus et al. 2017). With regard to the robusticity index, the second toes of both the Neandertal and Libben Native American samples differ significantly from the PP 654270 value, and the PP 654270 value also falls below the observed ranges of variation for the other fossil human samples. This suggests that the South African MSA humans may have possessed relatively gracile distal pedal phalanges in comparison to other *H. sapiens* populations in Eurasia.

The high value of the distal end index (M3b × 100/M2b) for PP 654270 indicates that it possesses a relatively narrower distal end than Neandertals. This is not unexpected given the tendency for Neandertal distal pedal phalanges to be characterized by broad apical tufts. This index in the comparative samples does not differ significantly among any of the samples, except for the Neandertals for Ray II. However, the bivariate analysis of distal breadth and distal height indicates that the PP phalanx is relatively narrower than the sample of Neandertals for Rays II and III (Figure 5D). This reiterates the fact that PP 654270 is significantly narrower distally than in Neandertals.

Examination of the metrical variables for the distal phalanges of the fourth and fifth toes in our fossil and recent comparative samples (Table S1) reveals that the PP 654270 values differ significantly from the means and/or are outside the ranges of variation for most of the variables. These results reinforce our consideration that the PP phalanx is unlikely to be a fourth or fifth toe. In addition, the Diepkloof (DRS-2) distal phalanx, which articulates perfectly with an intermediate phalanx, and is attributable to the fifth ray (Verna et al. 2013) differs noticeably from the larger (length, breadth and height) and more robust PP element.

4 | Discussion and Conclusions

Distal pedal phalanges are comparatively rare in the palaeontological record for *Homo*, with the majority of specimens attributable to Neandertals and fossil *H. sapiens*. The problem of small fossil inventories of these elements is compounded by the problem of correctly attributing non-hallucial elements to the correct ray. Although several distal manual phalanges are known from the MSA of South Africa (Klasies River Main Site, Sea Harvest, Die Kelders, and Sibudu), the only distal pedal phalanx published to date is the fifth toe (DRS-2) from Diepkloof Rock Shelter (Verna et al. 2013). This fossil, which dates to MIS 3, is younger than the PP 654270 distal phalanx from PP, which we attribute to Ray II or III. Although six lateral distal pedal phalanges are known for *H. naledi* (Harcourt-Smith et al. 2015), they are unfortunately not identified as to ray, and this very small-bodied species, whose phylogenetic affinities with *H. sapiens* are uncertain, is geochronologically much older than PP.

TABLE 2 | Raw dimensions (in mm) and indices of Pinnacle Point 654270 distal foot phalanx and the comparative samples for toe II and III.

	Pinnacle Point 654270	Neandertals		MPMH		UP		MH-HTH		MH-Lib		MH-SPab	
Toe	II–III?	II	III	II	III	II	III	II	III	II	III	II	III
M1—maximum length	**13.1***	13.0 ± 1.4 [10.9–14.3] (*n* = 6)	13.2 [12.7–13.7] (*n* = 2)	**11.2 ± 0.6 [10.8–12.1] (*n* = 4)**	11.4 [10.5–12.0] (*n* = 3)	10.0 [8.5–11.0] (*n* = 3)	11.4 [11.0–11.8] (*n* = 2)	10.8 ± 1.7 [7.4–17.0] (*n* = 167)	10.8 ± 1.8 [6.8–16.4] (*n* = 165)	—	—	11.7 ± 1.6 [9.5–14.5] (*n* = 15)	11.7 ± 1.8 [9.1–16.0] (*n* = 16)
M1a—articular length	**11.7***	11.9 ± 0.6 [11.2–12.6] (*n* = 4)	11.2 [11.1–11.4] (*n* = 2)	10.9 [10.6–11.3] (*n* = 2)	—	9.5 (*n* = 1)	9.6 (*n* = 1)	9.8 ± 1.6 [6.5–15.4] (*n* = 167)	9.8 ± 1.7 [6.3–15.4] (*n* = 164)	**8.7 ± 1.1 [6.9–10.4] (*n* = 14)**	**8.2 ± 1.2 [6.1–10.5] (*n* = 16)**	10.5 ± 1.5 [8.4–13.2] (*n* = 15)	10.6 ± 1.7 [8.2–15.3] (*n* = 16)
M2—mid-diaphyseal breadth	5.5	6.9 ± 0.8 [6.3–8.3] (*n* = 5)	6.5 [6.0–6.9] (*n* = 2)	6.6 [5.5–7.8] (*n* = 2)	6.3 [5.5–7.4] (*n* = 3)	6.1 [5.4–6.8] (*n* = 2)	6.0 [4.9–7.0] (*n* = 2)	5.2 ± 0.9 [3.2–7.7] (*n* = 166)	4.7 ± 0.7 [3.0–7.4] (*n* = 165)	6.6 ± 0.6 [5.8–7.4] (*n* = 14)	6.1 ± 0.9 [0.5–8.0] (*n* = 16)	4.9 ± 0.9 [3.5–6.6] (*n* = 15)	4.8 ± 0.8 [3.4–6.7] (*n* = 16)
M2a—proximal breadth	10.9	11.3 ± 1.4 [9.6–13.0] (*n* = 6)	10.5 ± 1.9 [8.1–12.6] (*n* = 4)	11.5 [9.2–13.0] (*n* = 3)	10.4 [9.8–11.6] (*n* = 3)	9.9 (*n* = 1)	9.6 (*n* = 1)	9.9 ± 1.1 [6.5–12.8] (*n* = 167)	9.2 ± 1.0 [2.5–9.7] (*n* = 165)	10.5 ± 0.7 [8.7–11.7] (*n* = 14)	9.9 ± 0.8 [8.6–12.0] (*n* = 16)	9.8 ± 0.8 [8.1–11.4] (*n* = 15)	9.8 ± 0.9 [8.5–11.5] (*n* = 16)
M2b—distal breadth	**7.9***	**10.4 ± 0.9 [9.6–11.7] (*n* = 5)**	9.4 [8.4–10.4] (*n* = 2)	8.6 [7.2–10.1] (*n* = 2)	8.2 [7.0–10.6] (*n* = 3)	7.7 (*n* = 1)	7.4 (*n* = 1)	7.4 ± 1.3 [3.2–10.9] (*n* = 167)	6.8 ± 1.2 [5.8–11.4] (*n* = 165)	7.5 ± 0.8 [6.1–8.6] (*n* = 14)	7.0 ± 1.1 [5.5–9.3] (*n* = 16)	7.5 ± 1.0 [5.7–8.8] (*n* = 15)	7.3 ± 1.4 [4.7–10.5] (*n* = 16)
M3—mid-diaphyseal height	5.3	6.2 ± 0.6 [5.4–7.0] (*n* = 6)	6.5 [5.8–7.2] (*n* = 2)	5.8 [5.3–6.4] (*n* = 2)	5.9 [5.2–6.6] (*n* = 3)	5.1 (*n* = 1)	5.1 [4.2–6.0] (*n* = 2)	4.8 ± 0.7 [2.9–6.5] (*n* = 166)	4.6 ± 0.7 [2.9–6.9] (*n* = 165)	5.5 ± 0.8 [3.9–6.7] (*n* = 14)	5.3 ± 0.6 [4.5–6.5] (*n* = 16)	4.9 ± 0.6 [4.0–5.7] (*n* = 15)	4.5 ± 1.0 [3.2–6.9] (*n* = 16)
M3a—proximal height	7.3	8.4 ± 0.9 [7.3–9.4] (*n* = 6)	8.8 [7.6–9.6] (*n* = 3)	6.5 [6.0–7.0] (*n* = 3)	7.2 [6.8–7.8] (*n* = 3)	7.5 (*n* = 1)	7.3 (*n* = 1)	6.8 ± 0.8 [4.9–8.8] (*n* = 167)	6.5 ± 0.8 [4.7–8.3] (*n* = 165)	6.9 ± 0.7 [5.3–8.0] (*n* = 14)	6.6 ± 0.6 [5.2–7.5] (*n* = 16)	6.9 ± 0.7 [5.6–8.1] (*n* = 15)	6.7 ± 0.6 [5.6–8.2] (*n* = 16)
M3b—distal height	5.0	5.6 ± 0.7 [4.8–6.3] (*n* = 4)	6.1 [5.3–6.8] (*n* = 2)	—	—	5.0 (*n* = 1)	4.8 (*n* = 1)	4.8 ± 0.7 [2.9–6.6] (*n* = 162)	4.8 ± 0.7 [3.0–6.2] (*n* = 159)	—	—	4.7 ± 0.7 [4.0–5.6] (*n* = 15)	4.5 ± 1.1 [2.9–7.7] (*n* = 16)
T7—proximal articular height	5.4	6.3 ± 0.9 [4.6–7.1] (*n* = 6)	5.9 [5.0–6.4] (*n* = 3)	5.9 [5.5–6.2] (*n* = 2)	6.3 [5.7–6.7] (*n* = 3)	—	—	5.0 ± 0.6 [3.6–6.7] (*n* = 167)	4.9 ± 0.6 [3.2–6.4] (*n* = 164)	5.8 ± 0.4 [5.0–6.4] (*n* = 14)	5.9 ± 0.5 [5.0–7.0] (*n* = 16)	5.3 ± 0.5 [4.5–6.2] (*n* = 15)	4.9 ± 0.6 [3.8–5.8] (*n* = 16)

(Continues)

TABLE 2 | (Continued)

Toe	Pinnacle Point 654270	Neandertals		MPMH		UP		MH-HTH		MH-Lib		MH-SPab	
	II–III?	II	III	II	III	II	III	II	III	II	III	II	III
T8—proximal articular breadth	8.4	9.7 ± 1.1 [8.5–1.4] (n = 6)	9.3 [7.6–10.9] (n = 3)	9.8 [8.9–10.7] (n = 2)	9.4 [8.8–9.8] (n = 3)	—	—	7.6 ± 0.8 [5.6–9.8] (n = 167)	7.1 ± 0.8 [5.0–8.8] (n = 164)	8.5 ± 0.5 [7.8–9.4] (n = 14)	7.8 ± 0.9 [6.8–9.5] (n = 16)	7.6 ± 0.8 [5.9–8.8] (n = 15)	7.3 ± 0.8 [6.0–9.1] (n = 16)
M3 × 100/M2 index	96.4	94.0 ± 11.2 [75.9–104.3] (n = 5)	100.8 [96.7–104.9] (n = 2)	91.5 [82.1–96.3] (n = 3)	94.5 [84.5–109.1] (n = 3)	96.2 (n = 1)	85.7 [85.7–85.7] (n = 2)	94.1 ± 14.3 [55.5–143.6] (n = 166)	99.4 ± 13.7 [70.1–137.6] (n = 165)	83.4 ± 10.8 [60.8–95.4] (n = 14)	87.6 ± 11.4 [70.3–108.3] (n = 16)	101.2 ± 16.4 [69.4–128.8] (n = 15)	94.0 ± 11.7 [68.5–110.4] (n = 16)
M3b × 100/M2b index	67.6	56.0 ± 5.5 [50.5–61.2] (n = 4)	65.1 [63.1–67.2] (n = 2)	64.7 (n = 1)	—	64.7 (n = 1)	64.9 (n = 1)	65.9 ± 10.3 [40.3–96.7] (n = 162)	71.2 ± 11.9 [48.0–123.1] (n = 159)	—	—	63.0 ± 7.5 [47.0–72.3] (n = 15)	62.1 ± 9.1 [44.4–73.0] (n = 16)
Robusticity index (100 × [(M2 + M3)/2]/M1a)	**46.2***	**54.8 ± 4.4 [48.8–58.7] (n = 4)**	57.8 [53.2–62.5] (n = 2)	56.5 [47.6–67.0] (n = 3)	61.7 [52.2–71.2] (n = 2)	55.1 (n = 1)	47.4 (n = 1)	52.5 ± 9.8 [28.8–83.1] (n = 166)	48.2 ± 9.8 [27.6–80.9] (n = 164)	**70.5 ± 12.1 [54.0–92.8] (n = 14)**	71.3 ± 12.9 [50.5–98.4] (n = 16)	47.8 ± 10.4 [36.8–72.1] (n = 15)	45.0 ± 12.9 [23.5–82.9] (n = 16)

Note: Statistical parameters and comparison with fourth and fifth toe of the comparative samples are provided in Table S2. Mean ± 1 SD, range [ ] and sample size (n) are shown. Bold letters and asterisk indicate significant differences with some of the samples (Z-score > 1.96 in absolute terms). Modern humans (MH-HTH, MH-Lib and MH-Spab) are pooled sex samples. Neandertal sample includes: Amud 1 (II, left; Trinkaus 1975), Kiik-Koba 1 (II and III, Right and left; pers. obs. from cast), La Ferrassie 1 (III, left; pers. obs. from original), Regourdou 1 RG34 (II, left; Pablos, Gómez-Olivencia, Maureille, et al. 2019), Shanidar 4 (II and III; Trinkaus 1983), Shanidar 5 (II?; Pomeroy et al. 2017), Sima de las Palomas SP92TT; (III; Trinkaus et al. 2017) and Tabun C1 (II, right; Trinkaus 1975). MPMH sample includes: Qafzeh 6 (II, left; Vandermeersch 1981), Qafzeh 8 (II and III, right and left) and Qafzeh 9 (II and III, right and left; Vandermeersch 1981), and Skhul 4 (II and III, right; McCown and Keith 1939; Trinkaus 1975). UP sample includes: Arancio 1 (III, left; Pardini and Lombardi Pardini 1981), Arene Candide 10 (II, right and left; Paoli et al. 1980), Mirón 1 (II right and left & III, right; Carretero et al. 2015) and Riparo Tagliente 1 (II, right and left; Corrain 1977).

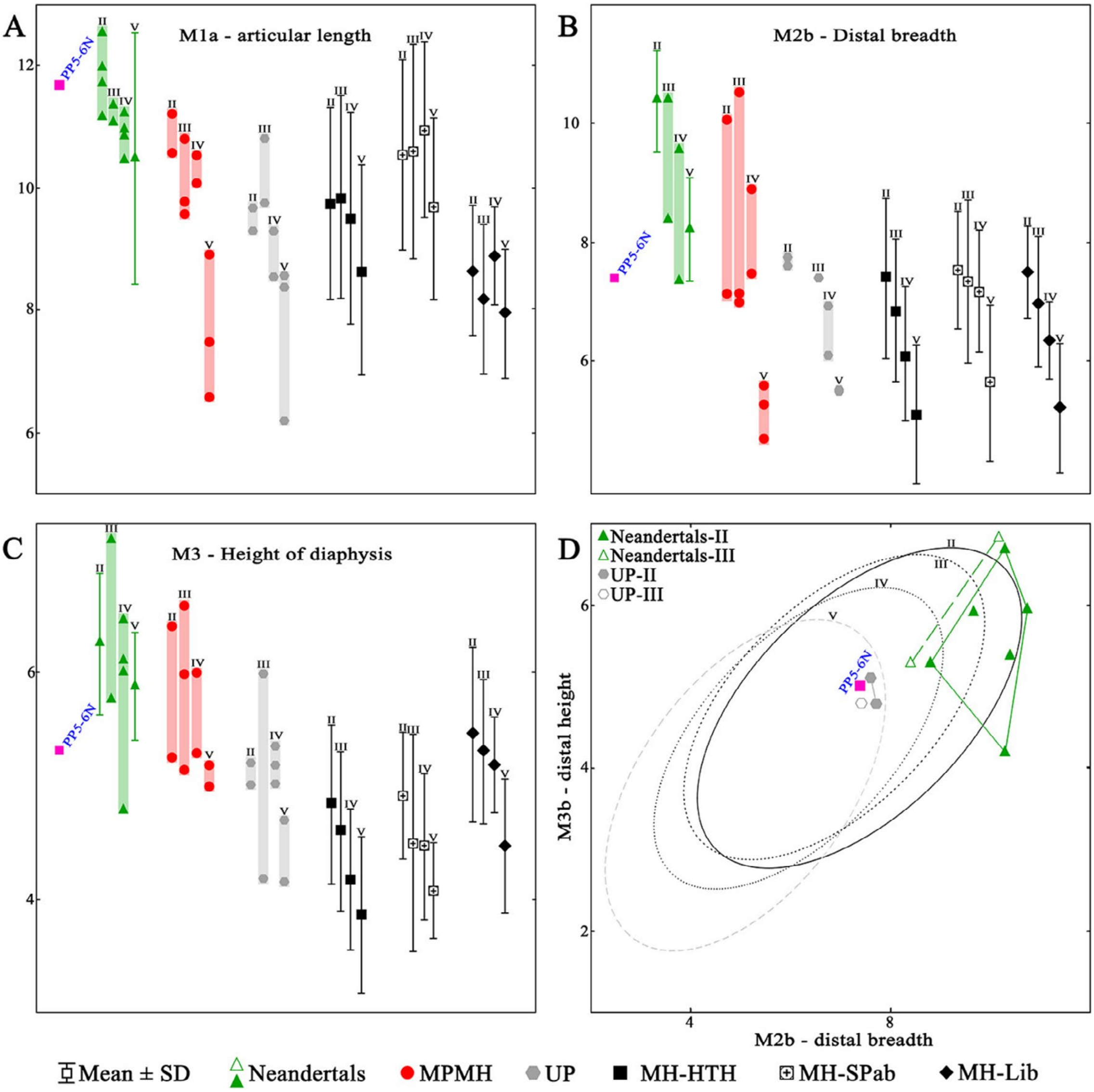

FIGURE 5 | Univariate metric assessment of the PP 654270 distal pedal phalanx. (A) Articular length (M1a). (B) Distal breadth (M2b). (C) Height of diaphysis (M3). (D) Bivariate analysis of the distal breadth (M2b) and height (M3b). MH-HTH, modern humans (MH)-Hamann–Todd collection; MH-Spab, San Pablo medieval collection; MH-Lib, unshod Libben Amerindians (from Trinkaus 1975); MPMH, Middle Paleolithic modern humans; UP, Upper Paleolithic modern humans. Mean ± 1 SD are shown. The Roman numerals in each figure indicate the pedal ray. All the variables are in mm. Note that all the graphs include second to fifth distal foot phalanges (indicated with Roman numerals) of the comparative samples except for the bivariate analysis that includes just the second and the third ones. The ellipses indicate the 95% equiprobability ellipses of the pooled recent modern human samples for each digit.

The distal pedal phalanx from PP is long, distally narrow, and generally gracile, especially in comparison with the broader and more robust Neandertal homologues. This difference may reflect differing biomechanical stresses or environmental influences on toe morphology in the Late Pleistocene of South Africa. The PP phalanx is not dissimilar to other fossil and recent *H. sapiens* phalanges from Rays II and III, and it is congruent with pene-contemporaneous Middle Paleolithic modern human elements from Eurasia. The archeological record of the MSA at PP indicates the prolonged exploitation of marine resources that would have been collected from the coast that would have been some 5–3 km from the site at the time that the individual to whom the PP 654270 phalanx belonged occupied the site at about 91.9–86.0 ka, with evidence of rather intensive mollusk collection and other coastal adaptations. The mammal fauna is indicative of active hunting, further emphasizing the probable high degree of mobility of the people inhabiting this coastal environment. The morphology of the PP distal phalanx is not inconsistent with the scenario reconstructed from the archeological record at the site.

Author Contributions

Adrián Pablos: conceptualization, investigation, methodology, writing – original draft, writing – review and editing, formal analysis. **Frederick E. Grine:** conceptualization, investigation, writing – original draft, writing – review and editing, formal analysis. **Naomi Cleghorn:** writing – review and editing, investigation, writing – original draft. **Katherine Elmes:** investigation, writing – original draft, writing – review and editing. **Carrie S. Mongle:** investigation, writing – original draft, writing – review and editing. **Curtis W. Marean:**

conceptualization, investigation, funding acquisition, writing – original draft, writing – review and editing, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The necessary data to support the findings of this study can be found in the main text and/or the Supporting Information. Measurement data have been provided in this article. Any other data generated in this study (e.g., 3D models) are available from the corresponding author, Frederick E. Grine or Curtis W. Marean, upon formal reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.