

22 **Abstract**

23 Based on the integration of laser scans, sedimentology, geochemistry, archeobotany, geometric
24 morphometrics and photogrammetry, here we present evidence testifying that a Palaeolithic group
25 of people explored a deep cave in northern Italy about 14 ky cal. BP. Ichnological data enable us to
26 shed light on individual and group level behavior, social relationship, and mode of exploration of
27 the uneven terrain. Five individuals, two adults, an adolescent and two children, entered the cave
28 barefoot and illuminated the way with a bunch of wooden sticks. Traces of crawling locomotion are
29 documented for the first time in the global human ichnological record. Anatomical details
30 recognizable in the crawling traces show that no clothing was present between limbs and the
31 trampled sediments. Our study demonstrates that very young children (the youngest about three
32 years old) were active members of the Upper Palaeolithic populations, even in apparently
33 dangerous and social activities.

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35 **Keywords:** human footprints; Upper Paleolithic; morphometric analysis; human locomotion;
36 cave use; finger flutings.

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44 **Introduction**

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46 Discovered in 1950, the hypogeal part of the ‘Grotta della Bàsura’ is a large and deep cave that
47 has produced some of the most important Italian Palaeolithic discoveries of the twentieth century
48 (Chiappella, 1953; Tongiorgi and Lamboglia, 1954; Blanc, 1960; Lamboglia, 1960; Giacobini,
49 2008) consisting of traces of human activity, especially footprints, dating back to 14 ky cal. BP. Up
50 till 1890 only the atrial part of the cavity was known where Neolithic and late Roman
51 archaeological finds had been unearthed (Maineri, 1985). The cave opening is situated at 186 m
52 a.s.l. about 1 km north of Toirano (Savona, Italy - 436253.433 E; 4887689.739 N), and extends 890
53 metres into Mount S. Pietro with an elevation difference of + 20 / -22 meters relative to that of the
54 entrance (Figure 1).

55 The inner rooms became accessible in 1950, after the rupture of a stalagmite column, placed a few
56 dozen meters from the entrance, that prevented any access to the cave (Tongiorgi and Lamboglia,
57 1954; Blanc, 1960; Lamboglia, 1960). The exceptional prehistoric and paleontological value of the
58 cave was firstly recognized by Virginia Chiappella (Chiappella, 1953) who was the first scholar to
59 visit the site soon after its discovery. Chiappella identified several bones of *Ursus spelaeus* and
60 traces both of animal and human frequentation (footprints, charcoals, digital tracks, lumps of clay
61 adhering to the walls) in different areas of the cave within approximately 350 m of the entrance.
62 Regrettably, destruction of most of the ichnological record occurred as a result of uncontrolled cave
63 visits by local villagers and tourists lured to the remarkable discovery as a result of media reports
64 (Blanc et al., 1960; De Lumley and Giacobini, 1985).

65 The first study of human footprints from the Cave of Bàsura was conducted by Pales (1960),
66 based on original images and 13 plaster casts of the best-preserved specimens from various sectors
67 of the cave. Analysis of the bone architecture of the footprint makers and the apparent relationship
68 with remains of *Ursus spelaeus*, led the author to consider that the footprints were made by

69 'Neanderthal-type' producers. Subsequent analysis (De Lumley et al., 1984), accompanied by
70 radiometric dating, placed the prehistoric visitation of the Bàsura in the Upper Palaeolithic, between
71 12,000 and 14,000 years uncal BP (De Lumley et al., 1984; De Lumley and Giacobini, 1985).
72 Dating of charred wood fragments found on the trampled surface provided a more precise age for
73 cave visitation at 12,340 years \pm 160 years BP (Molleson et al., 1972; Molleson, 1985).

74 Based on the ichnological study of Pales, Blanc proposed that the inner room called 'Sala dei
75 Misteri' was reached by multiple individuals, including a juvenile. Blanc (1960) described, from the
76 same room, a group of seven human footprints identified by heel tracks positioned only a few
77 centimetres from the main wall of the chamber to which numerous lumps of clay were attached.
78 The close association of the footprints with lumps of clay resulted in it being considered the result
79 of initiation rites involving young hunters. This hypothesis was supported by the presence of a
80 stalagmite concretion (defined by Blanc as '*acephalous sphinx*' or '*zoomorphic stalagmite*') placed
81 against the terminal wall of the "Sala dei Misteri" (Mysteries' Hall) chamber on which several
82 sinuous furrows had been made intentionally by several individuals using their fingers. This
83 interpretation is currently under review by two of the present authors (ES, MZ). The aim of this
84 work is to review and improve understanding of the Grotta della Bàsura's human ichnology, soil
85 micromorphology, sedimentology and radiocarbon chronology. A preliminary report from this
86 study focused on human footprints preserved in the innermost chamber of the cave (Citton et al.,
87 2017).

88 In the present paper, we expanded our study to analyze and interpret all human traces
89 (footprints and handprints as well as other traces) from the 'Grotta della Bàsura', providing new
90 insight on the behaviour, identity of the members, their exploratory techniques, and the social
91 structure of an Upper Palaeolithic group.

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95 **Data**

96 A total of 180 footprints and traces *sensu lato* were recorded and studied (Supplementary File
97 1). In addition to footprints (Figure 2), among the traces are digit and handprints on the clay-rich
98 floor, and smears from hands dirtied with charcoal on the side walls of the cave (Figure 3)
99 (Giannotti, 2008). A paleo-archaeological excavation was performed in 2016 in the “*Sala dei*
100 *Misteri*”. This survey highlighted the total absence of archaeological material but led to the
101 recovery, on the trampled palaeosurface, of numerous charcoal remains with bundles of *Pinus t.*
102 *sylvestris/mugo* originally used to illuminate the cave. New radiometric dating on these charcoal
103 samples constrains the exploration of the cave to the late Upper Palaeolithic, between 12,310±60
104 and 12,370±60 BP, that is from about 14.700 to 14.000 cal BP (Table 1).

105 Digit and hand traces are preserved in several sectors of the cave (Figure 3). Most are
106 unintentional traces related to cave exploration activities (Figure 3, C0, C26b, C72). Others,
107 especially in the inner chamber (‘*Sala dei Misteri*’) which are still being studied, are very probably
108 related to social or symbolic activities and can be instead considered intentional (Figure 3, SM55,
109 SM56). Moreover, different sized bear and *Canidae incertae sedis* footprints are ubiquitously
110 present (Figure 4), and are often associated with human prints. The available data regarding the
111 footprints attributed to “canids” suggest a very reduced number of individuals and a close
112 association with the human prints. Should ongoing studies (Avanzini et al in prep.) confirm that the
113 ichnological association of Bàsura could prove crucial to shed new light on dog domestication in
114 the Upper Paleolithic (Morey and Jeger, 2015; Perri, 2016; Lupo, 2017; Janssens, 2018).

115 *Ursus* sp. hibernation areas are still recognizable with well-preserved nests of both cubs and
116 adult bears.

117

118 **Preservation**

119 Footprints are preserved in several areas of the cave, particularly in the innermost chamber
120 (‘*Sala dei Misteri*’) and in the main gallery (‘*Corridoio delle impronte*’ – *Footprints Corridor*),

121 which is divided into two corridors at different elevations of about 5 m (respectively referred to as
122 the lower and upper corridor) (Figure 1).

123 Flooding dynamics and cave geometry produced two different situations for sediment
124 deposition and transport inside the cave. Detrital sediment comprising silty clay and well-sorted
125 sandy sediment are most abundant on the floor of the '*Sala dei Misteri*'. Coarse lithologies
126 comprising gravel-sized and larger (>2 mm) grains include a few fragments of bear bones. The
127 sandy fraction comprises allogenic, surface-derived siliciclastic sediment. The '*Sala dei Misteri*'
128 appears to have undergone episodic filling and erosion as a result of catastrophic storms.

129 Sediment in the '*Corridoio delle impronte*' comprises a large mud fraction and includes many
130 coarse lithic fragments which are mainly carbonates (calcite and dolomite), suggesting an autogenic
131 origin. Here, the trampled substrate is poorly consolidated and superimposed on a stalagmite crust.
132 At the time when humans and other large mammals left their traces the cave substrate differed in
133 different areas of the cave. In some areas, the substrate was plastic and in other areas it was
134 waterlogged or submerged. Differing moisture content of the substrate accounts for the variable
135 preservation of detail of the tracks (e.g. registration of plantar arch, heel and metatarsal regions,
136 digit tips, track walls), particularly of the associated extra-morphologies (e.g. expulsion rims,
137 slipping traces). The surface of the substrate and the footprints are cross-cut by mud cracks,
138 suggesting a loss of moisture in sediments after trampling. Carbonate crusts (comprising both
139 calcite and dolomite) cover many of the footprints in areas subjected to more intense dripping. Iron
140 and manganese oxide coatings were found in the crust, probably due to repeated immersion in
141 ponded water.

142

143 **Results**

144 Geometric morphometry performed on human footprints highlighted five main morphotypes
145 (hereafter Morphs.) indicating a possible minimum number of five individuals entering the cave
146 (Figure 5). This number is confirmed by the construction of morphological groups (Table 2)

147 reconstructed through the overlapping of footprints that show a variability of less than 2% of the
148 main parameters.

149 Morphs. 1 and 2 can be easily distinguished on the basis of the absolute footprint size. Morph.
150 1 includes footprints with a length of 13.55 ± 0.49 cm showing characters indicative of an early
151 ontogenetic stage of the producer, such as digit traces and the heel area proportionally wider than
152 those of the longer tracks. Morph. 2, with a length of 17 cm, is distinguished from Morph. 1 on the
153 basis of a more pronounced plantar arch. Morph. 3 comprises footprints 20.83 ± 0.51 cm in length
154 (Figure 5 and Table 3). The plantar area is characterized by a very pronounced medial embayment.
155 This corresponds with a strongly convex external margin, as is shared together with a strong
156 adduction of digit I trace, an overall larger divarication of digit traces and a consistent separation
157 between adjacent digits II-III and IV-V.

158 Morph. 4 (Figures 5, 6) is represented by larger footprints (22.80 ± 0.42 cm in overall length)
159 with roughly straight medial and lateral margins and a medial embayment less marked than that of
160 Morph. 3. Digit tip traces are strongly aligned and oriented forward. Morph. 5 (Figures 5, 7)
161 includes footprints of 25.73 ± 0.45 cm in overall length and slightly concave margins, with a variably
162 pronounced plantar embayment. The footprints of Morph. 5 are generally more robust and stockier
163 than those of Morphs. 3 and 4, sharing with Morph. 4 the straight, forwardly oriented digit tips, and
164 with Morph. 3 an adducted digit I trace.

165 Plantigrade tracks enabled us to estimate stature, weight and ontogenetic stage of the producers
166 based on biometric measurements (Table 3) and the adopted formulas (see Methods). An estimation
167 of the gender for Morph. 5 was also attempted (see Methods).

168 The group of human track producers entering the cave comprised: a three-year-old child about
169 88 cm tall (Morph. 1); a child at least six years old and about 110 cm tall (Morph. 2); a pre-
170 adolescent, between eight and eleven years old, about 135 cm tall (Morph. 3); a sub-adult to adult
171 about 148 cm tall (Morph. 4); and an adult about 167 cm tall (Morph. 5). Estimate of the stature for
172 the Morph. 5 is further supported by the length of the tibia derived from the available kneeling

173 traces (see Methods). Our results concerning Morphs. 4 and 5, which are referred to adult
174 individuals, are in agreement with the average stature of European Upper Palaeolithic people
175 (162.4 ± 4.6 cm for males and 153.9 ± 4.3 cm for females) (Villotte et al., 2017).

176 Body mass estimates derived from footprint parameters suggests slender and muscular body
177 proportions for all the trackmakers. Arch angle and footprint morphology suggests a male as the
178 probable trackmaker of the largest footprint group. Differently, the gender result difficult to infer
179 for morphotypes 1, 2, 3, 4, although Morph.4 can be referred most probably to a female.

180 Digitigrade and semi-plantigrade footprints provide information on pedal postures and the
181 behavior of the producers passing through different sub-environments of the cave. Both these
182 footprint types were, in most cases, traced back to the same type of producer by comparison with
183 complete footprints indicating complete foot support during locomotion. Some semi-plantigrade
184 footprints (e.g. Figure 8, C44, C44b) show a strongly adducted trace of digit I and an apparent
185 alignment with the other digits, probably because of the intra-rotation movements of the distal
186 portion of the foot during the thrust phase. Footprints included in the Morph. 3 show a peculiar
187 pedal morphology. While the resulting morphology of the digit I trace is explained by walking on a
188 waterlogged substrate, the separation between digit pairs II-III and IV-V suggest an inherited
189 familiar trait or a pathological condition of the producer's feet. The producer was not incapacitated,
190 showing the greatest mobility in the hypogeal environment.

191 In the lower corridor (Figure 9), a few of these footprints are associated with elongated traces
192 imprinted by the producers' knees resting on the substrate. Successions of kneeling traces can be
193 clearly recognized for Morphs. 3, 4, and 5. Based on the overall size of the metatarsal and knee
194 couples aligned on the substrate, crawling in a totally unknown environment is inferred for the
195 whole group. These knee imprints (e.g. Figure 8, C42) show the muscle structure of the knee joint
196 and adjacent regions. The patella, the patellar ligament (tendon), the tibial tuberosity, the fibular
197 head, the basis of the vastus medial and the iliotibial band are recognizable and allow us to infer the
198 body structure of the trackmakers.

199

200 **Discussion**

201 Successions of kneeling traces allowing one to infer a crawling locomotion for the trackmakers
202 have never been reported before. Isolated kneeling traces (i.e. a footprint followed by a knee
203 imprint of the same leg) have only previously been reported from the ‘Galerie Wahl’ at Fontanet
204 cave and from the ‘Salle des Talons’ at Tuc d’Audoubert cave, France (Pastoors et al., 2015) but are
205 not sufficient to infer crawling. In addition, the anatomic details clearly recognizable in the
206 crawling traces from ‘Grotta della Bàsura’ enabled us to hypothesize that no clothing was
207 interposed between the limb and the trampled sediments.

208 The integration of all available ichnological evidence with data on the complex morphology of
209 the cave enabled us to reconstruct a detailed hypothesis for the events which took place by
210 Paleolithic peoples while exploring the cave about 14,000 BP.

211 The short radiometric interval, documented by both previous radiocarbon dates and those
212 derived from the latest research presented here (Table 1), together with interferences relating to the
213 interrelations of the different footprints, suggest that all individuals entered the cave at the same
214 time. In particular, the group of footprints C34, C35b, C36, C35 in the terminal part of the
215 ‘*Corridoio delle impronte*’ provides relative timing of the impressions: C35 (Morph.4) is
216 superimposed on C36 (Morph.3) and on C34 and C35b (both Morph.5) (Figure 9, d3). In this
217 specific case, the producer of Morph.4 passed after the producers of Morphs 3 and 5, respectively.
218 In the entrance of the same corridor the timing is reversed: footprint C63 (Morph.4) is
219 superimposed by C64 (Morph.3) proving that Morphs. 3 and 4 were made at the same time (Figure
220 10).

221 It is also difficult to assume that Morphs. 1 and 2 may have entered the deepest part of the cave
222 without the presence of some older individual: if the older individuals who were leading the
223 exploration were either Morphs. 3 or 4 the group consequently increases to include at least 4
224 individuals. No relationship can be established for the larger individual; however, as reported

225 below, the fact that the footprints of this individual are regular and were closely followed on the
226 same path by all the other individuals, suggests that the larger one was likely the leader of the
227 synchronous exploration. Thus, all the available lines of evidence, particularly the complex
228 interrelationship of the studied footprints, strongly suggest that a single exploration event by a
229 heterogeneous group of five individuals is the most parsimonious and best supported hypothesis.

230 Five individuals, comprising two adults, an adolescent and two children, entered the cave
231 barefoot and with a set of *Pinus t. sylvestris/mugo* bundles which were burned for illumination
232 purposes. The adopted lighting system of several sticks enabled a longer period of lighting, as
233 inferred from the fire wood illumination bundles adopted by the Bronze age salt miners at Hallstatt
234 (Grabner et al., 2007, 2010). Lighting bundles were usually made of resinous wood (Scots pine or
235 Mountain pine), and called torch wood (Ast, 2001; Théry-Parisot et al., 2018). This interpretation
236 fits with the archaeological evidence from the Bàsura Cave.

237 After a walk of approximately 150 m from the original opening of the cave and a climb of
238 about 12 m, the group arrived at the '*Corridoio delle impronte*'. They proceeded roughly in single
239 file, with the smallest individual behind, and walked very close to the side wall of the cave, a safer
240 approach also used by other animals (e.g. *Canidae incertae sedis* and bears) when moving in a
241 poorly lit and unknown environment. The slope of the tunnel floor, inclined by about 24°, may have
242 further forced the individuals to proceed along the only flat area in the lower corridor, a couple of
243 meters from the left wall of the cave. About ten meters from the '*Corridoio delle impronte*', the
244 cave roof drops to below 80 centimeters and members of the group were forced to crawl (Figure
245 11B), placing their hands (Figure 12) and knees (Figure 8b) on the clay substrate (Figure 9) (see
246 also Video 1).

247 After a few meters, the group leader stopped, impressing two parallel calcigrade footprints,
248 possibly to decide on the next movement and proceeded to cross the parts where the cave roof was
249 at its lowest. The other individuals also stopped at the same place as the leader, and then proceeded

250 along the same path by crawling and following the group leader, as indicated by the timing
251 reconstructed from interactions between the tracks (Figure 9, d3).

252 After passing a bottleneck of blocks and stalagmites, the party descended for about ten meters
253 along a steeply sloping surface. The whole group traversed a small pond, leaving deep tracks on the
254 plastic waterlogged substrate, climbed a slope of 10 meters beyond the '*Cimitero degli orsi*', and
255 finally arrived at the terminal room '*Sala dei Misteri*', where they stopped. On the walls, several
256 charcoal traces, generated by the torches, are preserved.

257 Some charcoal handprints produced by a flexed reaching up more than 170 cm on the roof of
258 the '*Sala dei Misteri*' confirm that the tallest individuals (Morphs. 4 and 5) were able to touch this
259 part of the gallery. The fact that their footprints are not preserved relates to the loss of the central
260 portion of the hall floor. In the same room, the adolescent and children started collecting clay from
261 the floor and smeared it on a stalagmite at different levels according to height, as suggested by the
262 breadth and relative distribution of the finger flutings on the karst structure. During their sojourn in
263 the innermost room of the cave the young individual, that produced Morph. 2, imprinted ten clear
264 heel traces (Citton et al., 2017), which are here interpreted as calcigrade tracks produced by a
265 trackmaker who is momentarily standing-still to excavate and manipulate clay as was also recorded
266 for the '*Salle des Talons*' at Tuc d'Audoubert cave (Pastoors et al., 2015).

267 After stopping for several minutes (considering the quantity and ubiquity of the tracks), they
268 exited and followed a route which did not always adhere to that followed on entry. After passing the
269 small pond, they crossed the upper corridor following a more comfortable and safer route (Figure
270 11C). It is important to note that in the upper corridor all the prints point in the direction of the exit
271 (Figures 11C, 13) while in the lower corridor, with the axis of the foot oriented parallel to the walls,
272 most of the footprints are directed towards the interior of the cave.

273

274 **Concluding remarks**

275 A holistic analysis comprising several lines of inter-related ichnological evidence enabled
276 reconstruction of several snapshots depicting a small and heterogeneous group of Upper
277 Palaeolithic people that explored a cave about 14,000 years ago (Video 1). They traversed the
278 uneven topography of the cave floor and carried out social activities in the most remote room,
279 leaving evidence in their traces of a unique testimony to human curiosity.

280 The lower corridor was traversed on entry into the cave and documents the first unequivocal
281 evidence of crawling locomotion in the human ichnological record. This mode of locomotion was
282 adopted by the explorers to obviate variation in the height of the cave roof. As no outgoing
283 footprints were documented in the lower corridor it appears that the group chose to exit through the
284 upper corridor, as the cave roof is higher and the substrate firmer. An additional reason for choosing
285 this path of exit could have been the exploratory and curiosity factor to follow a different and
286 unexplored path to reach the cave exit.

287 Anatomical features clearly registered on the substrate indicate that the lower limbs of the
288 individuals were not covered with clothing. Our study also confirms that very young children
289 actively participated in the activities of the Upper Palaeolithic populations, even in seemingly
290 dangerous tasks, such as the deep exploration of the cave environment lit only with torches. As
291 recently suggested for other European caves (Pastoors et al., 2015, 2017; Ledoux et al., 2017) the
292 ‘Grotta della Bàsura’ site strongly supports the hypothesis that the cave exploration in Upper
293 Paleolithic was carried out by groups of heterogeneous age and gender.

294 The Epigravettian necropolis of the Arene Candide Cave (AMS dates spanning 12,820–12,420
295 cal BP for the first phase and 12,030–11,180 cal BP for the second phase), consisted of a “mixed”
296 sample of people (males, females, adults, children) and suggests an Upper Palaeolithic people
297 composition very similar to that highlighted in the ‘Grotta della Bàsura’ (Riel-Salvatore et al., 2018;
298 Sparacello et al., 2018). The burial of a newborn infant, together with grave goods, recently
299 discovered in the Arma di Veirana cave (Erli, Savona, Liguria) situated in a valley 10 km from the
300 coast, further indicates that women and children systematically followed the movements of the

301 group in the territory (F. N. pers. obs.) (Negrino et al., 2017) and shared, at least in part, the
302 activities of men and had similar personal adornment. The tracks left in the Bàsura indicate that the
303 behavior of hunter-gatherers was not always driven by subsistence requirements, but as manifested
304 by many ethnographic examples, also by fun and frivolous activities.

305

306 **Material and Methods**

307 **Chronology**

308 Radiometric dating of charcoals previously established the presence of humans in the cave to
309 the Upper Palaeolithic, around 12,340±160 years BP (De Lumley and Giacobini, 1985). The
310 stalagmite crust preserving the footprints and incorporating fragments of coal is dated to between
311 14,300±800 and 13,100±500 (Yokoyama, 1985). The final phase of stalagmite growth, which
312 closed the entrance and sealed the ‘time capsule’, occurred at 12,000±1100 (Yokoyama, 1985).

313 New radiometric dating of charcoal samples of *Pinus t. sylvestris/ mugo* was undertaken in
314 2017 at a AMS facility at Groningen (NL) on (Table 1). Material was collected from the trampled
315 palaeosurface during recent excavations inside the “*Sala dei Misteri*” (Figure 14).

316

317 **Laser Scanning acquisition**

318 Documentation of the sequence of events was contextualized and visualized on the rough cave
319 topography through three-dimensional mapping of the cave performed by laser-scanning. The main
320 landmarks of the cave were digitally recorded using the laser scanner ScanStation2 Leica and
321 ScanStation C10 Leica. The scans were performed at 360° (acquisition grid of the point cloud of
322 2x2 cm a probe 7 m and in correspondence to the areas with the highest concentration of traces, an
323 acquisition grid of 0.5x0.5 cm probe 7 m). In total, 23 stations were run (9 in the ‘*Sala dei Misteri*’
324 and 14 in the ‘*Corridoio delle impronte*’ areas); 38 targets (16 in the ‘*Sala dei misteri*’ and 22 in the
325 ‘*Corridoio delle impronte*’) were used for the point clouds registration. The Leica Geosystems HDS
326 Cyclone 9.1 software was used to process the data. The recording shows a final alignment error of 2

327 mm for the model of the *'Sala dei Misteri'* and 1 mm for the *'Corridoio delle impronte'* (Video 1).
328 From the models, reliefs were obtained at various degrees of detail that enabled georeferencing of
329 all traces. The original cast performed in 1950 were digitally acquired via HDI Advance structured-
330 light 3D Scanner R3x, with a resolution of 0.25 mm at 600 mm FOV (field of view). The data were
331 processed with FlexScan3D Software (Figures 6, 7, 8d, 9d).

332

333 **Digital Photogrammetry**

334 Several photogrammetric models were obtained using several photos taken with 24 Megapixel
335 Canon EOS 750D (18 mm focal length). The software used to build models is Agisoft PhotoScan
336 Pro, (www.agisoft.com). High resolution Digital Photogrammetry is based on Structure from
337 Motion (SfM) (Ullman, 1979) and Multi View Stereo (MVS) (Seitz et al., 2006) algorithms and
338 produces high quality dense point clouds. The accuracy of the obtained models is up to 1 mm for
339 close-range photography. The reconstructed 3D surfaces were then processed in the open-source
340 software Paraview. False coloured models with contour lines, highlighting general morphology and
341 differential depth of impression of the traces, were obtained (Figures 9a, 12, 13).

342

343 **Analysis of human footprints**

344 All recognized tracks (107 human traces) were analyzed directly in the field through a
345 morphological approach using available landmarks (Robbins, 1985). The differential depth of each
346 individual impression was analyzed directly in the field to infer the complex and multiphase
347 biomechanics. All isolated footprints, and those associated with trackways, were drawn in the field
348 on plastic film. All morphological and dimensional data collected in the field were double-checked
349 by using photos and photogrammetric models.

350 In addition, the original casts of the footprints from the 1950s were also used and analyzed.
351 Their positions in the cave were verified and it was established that all the footprints identified
352 during the early explorations are still visible *in situ* (Figure 1, Table 4). Some of them have suffered

353 alteration and loss of detail and others have been partially damaged. For this reason in some
354 instances we have integrated morphometric data of the *in situ* footprints with those of plaster casts.
355 In addition the following two indices were considered: Footprint index (FI), equal to foot width/foot
356 length x100 and Arch angle (Aa), represented by the angle between the footprint medial border line
357 and the line that connect the most medial point of the footprint metatarsal region and the apex of the
358 concavity of the arch of the footprint (Clarke, 1933). In the reconstruction of body dimensions and
359 age, only the foot measurements derived from the better-preserved footprints were used (Table 3).

360

361 **Principal Component Analysis**

362 The 23 better preserved footprints were subjected to a Principal Component Analysis (PCA)
363 using the software PAST 3.10 (Hammer et al., 2001). Homologous points were selected on the
364 footprints for the measurements (Robbins, 1985) (Figure 15). These included nine anatomical
365 lengths and widths (foot lengths (Dt1-BL, Dt2-BL, Dt3-BL); ball medial length (mtm-BL); ball
366 lateral length (mtl-BL); heel medial length (ccm-BL); heel lateral length (ctul-BL); widths of ball
367 (mtm-horiz.) and heel (ctul-horiz.) (Table 4). The raw data were log-transformed before the analysis
368 to fit linear models and for the correspondence of the log transform to an isometric null hypothesis
369 (Chinnery, 2004; Cheng et al., 2009; Romano and Citton, 2015, 2016; Romano, 2017). Missing
370 entries were treated according to the ‘iterative imputation’ in PAST 3.10, preferable to the simple
371 ‘mean value imputation’ (Hammer, 2013). The results of the PCA are reported in the scatter plots of
372 Figure 5a whereas the loadings for the first three principal components are provided as
373 supplementary information (and Appendix 1 Tables A, B, Figure 5-figure supplement 1).

374

375 **Stature**

376 It is possible to estimate stature from foot length (Robbins, 1985; Oberoi, 2006; Krishan and
377 Sharma, 2007; Kanchan et al., 2008; Pawar and Pawar, 2012). Stature varies with race, age, sex,
378 heredity, climate and nutritional status. Based on skeletal evidence it is thought that the body

379 proportions of terminal Upper Palaeolithic individuals was similar to that of modern humans
380 (Trinkaus, 1997; Ruff et al., 2005; Shackelford, 2007) but the foot length/stature ratio was
381 considered highly uncertain, between 0.15 and 0.16. Consequently, we calculated the foot
382 length/stature ratio based on a sample of terminal Upper Palaeolithic adult individuals (n.8) from
383 the Italian Peninsula (Corrain, 1977; Paoli et al., 1980; Formicola et al., 1990; Mallegni and Fabbri,
384 1995; Mallegni et al., 2000). The calculated ratio is found to be 0.1541, which is close to those
385 proposed for modern humans between the XIX and XX centuries (Robbins, 1985; Topinard, 1978).
386 Stature estimation from the length of long bones is commonly used in forensic medicine. In this
387 study, we used the percutaneous length of the tibia to check the stature of the Morph. 5 as this
388 measurement is known to have a strong correlation with body height. We used the relation $S =$
389 $101.85 + 1.81 \times \text{PCTL} \pm 3.73$ for male and $S = 77.86 + 2.36 \times \text{PCTL} \pm 2.94$ for female (where $S =$
390 stature and PCTL = Percutaneous tibial length) (Lemtur et al., 2017). For a tibial length of 35 cm,
391 the stature of Morph. 5 is 165.2 ± 3.73 cm, which is comparable to the stature assumed from foot
392 length (166.99 ± 2.93 cm).

393

394 **Body mass**

395 Body mass estimates were derived from footprint parameters, based on the assumption that
396 human body proportions have been constant through time (Dingwall et al., 2013). Regression
397 formulae are based on mature individuals ranging between 154 and 185 cm in stature (Weight
398 $\text{Kg} = 4.71 + (1.82 \times \text{FL})$) (Dingwall et al., 2013; Bavdekar et al., 2006; Ashton et al., 2014) or on
399 children (Grivas et al., 2008) with an average height of 147,44 cm (weight $\text{Kg} =$
400 $71.142 + (5.259 \times \text{righthFL})$). We have used these formulae for the individual taller than 147 cm (Table
401 3), stature: (b) (Bavdekar et al., 2006), (c) (Grivas et al., 2008). For the three smaller individuals we
402 used formulae based on extant Caucasian children between 6 and 11 years old (n. 7147) ranging in
403 stature between 118.6 and 145.7 cm (Malina et al., 1973) to develop a mathematical relation
404 between foot length and body mass for young individuals. The report is nonlinear and expressed by

405 the formula $mass = 2.2897 e^{0.126FL}$ (Citton et al., 2017). No dataset are available for the smaller
406 individual. We have therefore hypothesized the body mass of MP1 by the trend-line derived from
407 previous formulae.

408

409 **Age**

410 Foot length varies according to age and gender. Studies on the relationship size/age of the foot
411 in extant juvenile individuals (Fryar et al., 2012; Müller et al., 2012) have highlighted that one year
412 old individuals have a foot length equal to 13.07 ± 1.59 cm, reaching 24.4 ± 2.96 cm at the age of
413 13 years. The age estimation based on growth curves built on extant populations is very similar.
414 However, we must bear in mind that the reference anthropometric data mainly refer to modern well-
415 nourished populations, with a body mass most likely higher at the same age. Anthropometric
416 studies suggest that the morphology of the foot changes and becomes more elongated when the arch
417 stabilizes around the age of six (Müller et al., 2012). In extant human populations, from the fifth or
418 sixth years of age, arch angles vary from 21° (3-4 years) to 43° (9-11 years) in young males, and
419 from 26° (3-4 years) to 47° (9-11 years) in young females (Forriol and Pascual, 1950). As a result,
420 morphotypes 2 and 3 seem to be similar, likely suggesting a corresponding similarity of age
421 between producers of the two morphotypes. Growth curves based on extant populations with an
422 average height similar of those of the Late Upper Paleolithic provided an estimate of the age of the
423 trackmakers. For MP5 the wide and stout morphology is here interpreted as an adult stage with the
424 partial collapse of the plantar arch.

425

426 **Gender**

427 Sex determination established from the foot has been proposed using Foot index and threshold
428 values. However, this approach is not entirely accepted and some researchers pointed out that the
429 threshold value could vary significantly between populations, thus making it very speculative that
430 gender estimations could be determined from foot morphology (Walia et al., 2016). These

431 variations could be due to fact that anatomic structures of the foot manifest ethnic and regional
432 variations owing to climatic factors, physical activities, socio-economic status and nutritional
433 conditions. Despite the method, uncertain arch angle and footprint morphology suggests a possible
434 male as trackmaker of the largest footprint group. No definitive gender can be inferred for
435 Morphotypes 1, 2, 3, 4.

436

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609

610 **Figures**

611 **Figure 1. Planimetry of the ‘Grotta della Bàsura’ and location of human, bear and canid footprints.**
612 White rectangles enclose the three-dimensional reconstructions, obtained via laser scanner, of the innermost
613 room (‘Sala dei Misteri’ - left) and the main gallery (‘Corridoio delle impronte’ - right) of the cave, where
614 the human footprints are preserved. Cross-sections obtained from the three-dimensional reconstruction of the
615 main gallery are highlighted in red and show the branching of the ‘lower’ and ‘upper’ corridors, respectively.
616 Blue rectangle indicate the four areas within the main gallery where most of the human footprints are
617 concentrated (A and B for the lower corridor, C and D for the upper corridor).

618
619 **Figure 2. Human footprints imprinted on muddy substrate in different moisture conditions.** C37,
620 Human footprint referred to the Morph. 5 (‘lower corridor’). CA1 and C9, Human footprint referred to the
621 Morph. 4 (‘upper corridor’). C33, Human footprint referred to the Morph. 3 (‘lower corridor’). SM15,
622 Human footprint referred to the Morph. 3 (‘Sala dei Misteri’). CA8, Human footprint referred to the Morph.
623 3 (‘upper corridor’). SM5 and SM42, Human footprint referred to the Morph. 2 (‘Sala dei Misteri’). SM17
624 and SM18, Human footprint referred to the Morph. 1 (‘Sala dei Misteri’).

625
626 **Figure 3. Finger and hand prints.** C0, Two finger traces on the concreted side-wall of the ‘lower
627 corridor’. C26b, Finger traces (‘lower corridor’). C72, Hand print (‘lower corridor’). SM44, finger traces
628 (‘Sala dei Misteri’). SM55, Finger flutings on the clay on the clay floor (‘Sala dei Misteri’). SM56, Finger
629 flutings on a clay-coated stalagmite (‘Sala dei Misteri’). P8.1, P1.6, Coal dirtied handprints (‘Sala dei
630 Misteri’).

631
632 **Figure 4. Canidae incertae sedis and bear footprints.** C47-C48-C53 Canidae footprint on saturated mud
633 (‘upper’ corridor). CA12 well preserved Canidae footprint (‘upper corridor’). SM12-SM41 bear footprint
634 (Sala dei Misteri). C12 bear handprint (‘lower corridor’).

635
636 **Figure 5. Principal Component Analysis based on the best-preserved footprints from ‘Sala dei Misteri’**
637 **and ‘Corridoio delle impronte’.** a, The five morphotypes to which footprints have been referred are shown
638 above. b, Selected outlines of the best preserved footprints, for each recognized morphotype, are reported.

639 **Figure 6. Plantigrade tracks from the ‘lower corridor’.** a, cast of the 1950s reproducing tracks C61, C63
640 and C64, preserved in the sector A of the ‘lower corridor’ (see Fig. 1 main text). b, Digital terrain model of
641 the cast obtained from the HDI 3D Scanner. c, Topographic profile with contour lines, obtained from b. d,
642 Interpretive draw. Note that the tracks C61 and C63 were most likely left by a producer (Morph. 4)
643 crouched against the side-wall of the ‘lower corridor’.

644 **Figure 7. Plantigrade track from the ‘lower corridor’.** a, cast of the 1950s reproducing the track C60 pre-
645 served in the sector A of the ‘lower corridor’ (see Fig. 1 main text). b, Digital terrain model of the cast ob-
646 tained from the HDI 3D Scanner. c, Topographic profile with contour lines, obtained from b. d, Interpretive
647 draw. A superimposed partial canid track, C60b, is clearly recognizable in the metatarsal area of the human
648 footprint (Morph. 5).

649
650 **Figure 8. Selection of semi-plantigrade and knee traces from the ‘lower corridor’ of the ‘Corridoio**
651 **delle impronte’ in the Bàsura cave, indicating crawling locomotion of the producers.** a, Associated
652 metatarsal (C44) and knee (C45) traces allowing estimation of the tibial length of the producer. b, Knee
653 traces (C45, C42 and C41) imprinted on a plastic, waterlogged muddy substrate. c, Metatarsal traces (C26,
654 C44 and C44b) imprinted on a plastic, waterlogged muddy substrate. d1, cast of the 1950s reproducing two
655 knee (C41 and C42) and two metatarsal (C44, C44b) traces preserved in the area B of the ‘lower corridor’

656 (see Fig. 1). **d2**, Digital Terrain Model obtained from the HDI 3D Scanner. **d3**, Topographic profile with
657 contour lines, obtained from d2. **d4**, Interpretive draw. In the knee trace C42 are located the impressions of
658 the patella (a), vastus medialis (b), the fibular head (c), the patellar ligament (d) and the tibial tuberosity (e).
659

660 **Figure 9. Crawling locomotion in the ‘lower corridor’ (sector B in Fig. 1).** **a**, Colour topographic profile
661 obtained from the digital photogrammetric model. **b**, Topographic contoured profile. **c**, Interpretive draw of
662 the track-bearing surface (numbers identify single tracks and traces and are to be intended as preceded by the
663 letter C). **d1**, Digital Terrain Model obtained from a cast of the 1950s reproducing a small area of the ‘lower
664 corridor’. **d2**, Topographic profile with contour lines, obtained from d1. **d3**, Interpretive draw and timing of
665 the different recognized tracks.
666

667 **Figure 10. Timing of impressions of human footprints.** The interference between footprints attributed to
668 different individuals suggests a single exploring event of the cave. In particular the cross-overlapping of
669 MP3 and MP4 trackmakers confirms their contemporary entry into the main gallery.
670

671 **Figure 11. Reconstruction of the exploration routes chosen by the producers to enter and exit the cave.**
672 **B**, Crawling locomotion adopted by the producers to cross the ‘lower corridor’ and access to the innermost
673 rooms of the cave. **C**, Exit route passing through the ‘upper corridor’, traveled by the producers in complete
674 erect walking. The smallest producers are not reported in the sketch.

675 **Figure 12. Human tracks from the ‘lower corridor’.** **a**, Tracks C26, C26b, C25 and C24 from the sector B
676 of the ‘lower corridor’ (see Fig. 1 main text). **b**, Digital terrain model obtained from high-resolution photo-
677 grammetry. **c**, Topographic profile with contour lines, obtained from b. **d**, Interpretive draw. C26b is inter-
678 preted as a partial hand-print of which only digit traces are preserved, interfering with a metatarsal trace
679 deeply imprinted on a muddy, highly plastic, substrate.

680 **Figure 13. Shallow human tracks from the ‘upper corridor’.** **a**, Tracks CA8, CA9, CA10 and Ca11b
681 from the sector C of the ‘upper corridor’ (see Fig. 1 main text). **b**, Digital terrain model obtained from high-
682 resolution photogrammetry. **c**, Topographic profile with contour lines, obtained from b. **d**, Interpretive draw.
683 Tracks were impressed on a hard carbonate substrate covered by a thin muddy deposit, few millimeters in
684 thickness.

685 **Figure 14. Profile and map of the archaeo-paleontological excavations in the Mysteries Hall (left), soil**
686 **micromorphology sampling and view of the excavations (right).** The sampled charcoal for dating are
687 highlighted by a red dot.

688 **Figure 15. Adopted landmarks utilized to perform morphometric analysis, showed in two distinct**
689 **morphotypes (Morphs 3 and 4) as example.** Landmarks in the distal portion of digit traces 4, 5, and in the
690 medial, central and lateral portions of the sole trace were not considered reliable enough for the large varia-
691 bility, higher than the fixed error value (± 0.5 cm).
692
693

694 **Tables**

695

696 **Table 1. Radiometric dating of charcoals collected from the trampling palaeosurface during 2017 excavations inside the ‘Sala dei misteri’**697 (*¹⁴C ages have been calibrated to calendar years with software program: OxCal, version 4.3. Used calibration curve: IntCal13)

698

SAMPLE NAME	PROVENANCE	DATED MATERIAL	DESCRIPTION	LAB. CODE	F ¹⁴ C ± 1σ	¹⁴ C AGE (yr BP) ± 1σ	CALIBRATED*			δ ¹³ C (in ‰; ±1σ)	δ ¹⁵ N (in ‰; ±1σ)	C/N ratio
							DATING RESULT (95.4 probability)	%C	%N			
Bàsura SM B5 17B	‘Sala dei misteri’, square B5, Unit 1	charcoal (AAA)	<i>Pinus t. sylvestris/mugo</i>	GrA-69598	0.2160±0.0016	12310±60	12720–12110 cal BC	71.4	-	-25.24±0.14	-	-
Bàsura SM D6 33B	‘Sala dei misteri’, square D6, Unit 1	charcoal (AAA)	<i>Pinus t. sylvestris/mugo</i>	GrA-69597	0.2145±0.0016	12370±60	12830–12165 cal BC	63.3	-	-26.37±0.14	-	-

699

700

Table 2. Footprint shape features after “Robbins footprint recording form” (1985, p.97-102).

ID	Left (L) or right (R) foot	General appearance		Relative length of toes	Toes region general appearance length - width	Toe 1 position	Ball region, general appearance length-width	Arch region		Heel region, general appearance	Hell posterior margin	
		Length	Width					Medial margin	Lateral margin			
SM3	R	short	broad	1, 2, ?	short - broad	extended, anteriorly		straight	concave	circular	convex pronounced	Morphotype 1
SM4	L			1,2,3,4,5	short - broad	extended, anteriorly	short - moderate		concave			
SM43	L	short	broad	1,2, ?	short - broad	extended, anteriorly		straight	convex		convex pronounced	
SM17	R	short	broad	1,2,3,4,5	short - broad	extended, anteriorly		straight/concave	convex		convex pronounced	
SM5	R	moderate	moderate	1,2,3,4,5	short - broad	extended oblique medially	long - moderate	concave	concave		convex slight	Morphotype 2
SM42	R	moderate		1,2, ?		extended oblique medially		concave			convex pronounced	
SM26	L	moderate	broad	1,2,3,4,5	short - moderate	extended oblique laterally		concave	concave		convex slight	
CA8	R	long	moderate	1,2,3,4,5	moderate - broad	extended oblique medially	long - moderate	concave	straight	oblong	convex pronounced	Morphotype 3
CA10	R	long	moderate	1,2,3,4	moderate - broad	extended oblique medially		straight/concave	straight	oblong	convex pronounced	
SM15	L	long	moderate	2,3,1,4,5	moderate - broad	extended oblique medially	long - narrow	concave	straight	oblong	convex pronounced	
SM11	R	long	moderate	1,2,3,4,5	short - broad	extended anteriorly		straight/concave	convex	oblong	convex pronounced	
SM6	L	long	moderate	2,1,3,4,5	short - broad	flexed slight	long - narrow	concave	convex	oblong	convex pronounced	
SM1	L	long	moderate	2,3,1,4,5	short - broad	extended oblique medially	moderate - narrow	unknown	convex	circular	convex pronounced	
C33	L	long	broad	1,2,3,4,5	long - broad	extended oblique medially	long - broad	concave	convex	oblong	convex pronounced	
C36	L	long	very narrow	1,2,3,4,5	moderate - narrow	extended oblique laterally	long - narrow	concave	straight	oblong	convex pronounced	
CA1	R	long		1,2,3,4	moderate - broad	extended anteriorly	moderate - narrow	straight		oblong	convex, pronounced	Morphotype 4
CA2	L	long	moderate	1,2,3,4,5	moderate - broad	extended anteriorly	moderate - narrow	concave	straight	oblong	convex pronounced	
C61	L	long	moderate	1,2,3,4,5	moderate - broad	extended oblique medially	moderate - narrow	straight/ concave	straight/convex	oblong	convex pronounced	
C63	R	long	moderate	1,2,3,4,5	moderate - broad	extended anteriorly	moderate - narrow	straight/ concave	straight/concave	oblong	convex pronounced	
M21	R	long	moderate	1,2,3,4,5	moderate - broad	extended anteriorly	moderate - narrow	concave	straight	oblong	convex pronounced	
C9	R	long	moderate	1		extended anteriorly	moderate - narrow	straight	convex	oblong	convex pronounced	
C44b	L	long	broad	2,1,3,4,5	short - broad	extended oblique medially	moderate - broad	concave	convex	oblong	convex, moderate	
C60	L	long	broad	1,2,3,4,5	moderate - broad	extended oblique laterally	moderate - broad	straight/ concave	straight/ concave	circular	convex moderate	Morphotype 5
C37	L	long	broad	1,2,3,4,5	moderate - broad	extended anteriorly	moderate - broad	straight/ concave	straight/ concave	circular	convex moderate	
C35b	R	long	broad	1,2,3,4,5	moderate - broad	extended anteriorly	moderate - broad		straight/ concave	circular	convex moderate	
C44	L	long	broad	1,2,3,4,5	moderate - broad	extended anteriorly	moderate - broad	concave	straight/ concave	oblong	convex pronounced	

Table 3. Measurements and elaboration data (foot index, stature, body mass and age) based on the best-preserved tracks from the ‘Sala dei Misteri’ and ‘Corridoio delle impronte’. *Body mass: (a) Citton et al. 2017; (b) Bavdekar et al. 2006; (c) Grivas et al. 2008 (see text).

ID	Left (L) or right (R) foot	LENGTHS										WIDTHS			ANGLES	max FL (cm)	max FW (mtm- mtl) (cm)	arc angle (degrees)	Foot index	stature (cm)	body mass * (kg)	age	
		FOOT					BALL		ARCH		HEEL		BALL	ARCH	HEEL								T1-T5 Angle of toe declination (degrees)
		Dt1 (cm)	Dt2 (cm)	Dt3 (cm)	Dt4 (cm)	Dt5 (cm)	medial (mtm- BL) (cm)	lateral (mtl- BL) (cm)	medial (ntu- BL) (cm)	lateral (mttu- BL) (cm)	medial (ccm- BL) (cm)	lateral (ctul- BL) (cm)	mtm- horiz (cm)	mttu- horiz (cm)	ctul- horiz (cm)								
SM3	R	13	12,3				10,5	9,2	5,5	6,8	2,3	2,4	5,5	4,7	4,3								
SM4	L	13,5	12,5	11,5	11	9,8	10,2	8	4	5,5	2,2	1,6	5,5	4	4,2	40							
SM43	L	13,5	13,5				10,5	9,4	5,5	6,5	2,2	1,8	6	5,5	4,6								
SM17	R	14,2	13,8	13,5	12,6	10,8	10,2	8,5	5	6	2	1,8	6,5	4,8	4	32							
															13,55±0,49			0,48±0,01	87,93±3,20	12,64±0,79^(a)	< 3	Morphotype 1	
SM5	R	17	16,8	15,5	14	13	12	12			2,5	2	6,5	5	35								
SM42	R	17	16,8				12,5	11,5		10	3,4	2,5	7		5,4								
SM26	R	18	16,5	15	14						2	3			5								
															17			0,41±0,02	110,32	19,5^(a)	5-6	Morphotype 2	
CA8	R	20,2	19,8	19,4	18,3	16,8	15	13	7,5	9,2	2,6	2	7,5	6	4,5	30							
C10	R	20,5		19,2	18,4	16,5	15,5	12,5	6,5	8,5	2,8	2,6	7	5,5	5,6	32							
SM15	L	20,5	20,5	18,5	17,5	16	15,4	13	6,5	7,8	4	2	7	4	6	30							
SM11	R	21	20,2	19,7	18	16,8	15,4	14,5	5,5	8	3,3	2,3	7,5	6,8	6	30							
SM6	L	21	21,5	20,5	18,8	17	17,5	15,5	6,8	8,5	4	2,2	9,2	5,5	5,7	20							
SM1	L	21,2	21,3	20,8	20,4	18,5	17,4	14,8	6,8	8,7	3,8	2,5	8	5	6	20							
C33	L	22,2	21	19,5	17,3	14,8	15,5	10,7	6	7,8	2,5	2	10	6,5	5,8	45							
C36	L	22,7	21,7	19,5	17,8	16,2		14,5			3	2,5			5,5	48							
															20,83±0,51			0,38±0,03	135,19±3,33	31,66±2,05^(a)	8-11	Morphotype 3	
CA1	R	22,4	21,8	20,8	18,5		14,8	12,8	7		3,1		8										
CA2	L	22,5	22	21	20	18,5	17,3	15,2	6	8,6	3,5	3,5	8,8	6	6,4	30							
C61	L	23	21,7	20,8	20	19,5	16,4	14	8,5	9,5	3,8	3	7,5	6,5	5,4	30							
C63	R	23,3	22,2	20,8	19,8	18,7	17	14	7,9	9,5	3,5	3,8	8,5	6,7	5,3	32							
M21	R	-	21,6	21,3	20,7	19,2	16,7	14,6	7,8	10,5	3,5	2,4	9,6	4,8	6,2								
C9	R	22,5											8		5,5								
C44b	L	21,5	21	20	19,5	18,5	15	13	7	4	2,2	1,5	10	5	5,5	20							
															22,80±0,42			0,38±0,01	147,96±2,75	46,21±0,77^(b) - 48,76±2,23^(c)	> 14 - adult	Morphotype 4	
C60	L	25,3	24,2	22,7	21,4	20	18	14,8	6	8	3,5	3,3	10,5	7,5	6,4	35							
C37	L	25,7	23,8	22,5	21	19,5	18,4	14,7	6	7,8	3,7	3,5	10,5	7,5	7	35							
C35b	R	26,2	24,8	22,8	20,7	18,7	17	13,7	5,8	7,2	3,7	2,7	9,5	7	6,7	40							
C44	L	25	23,5	22,5	20,8	19	16,8	14,2	5,5	6,7	2,8	2	9,2	5,7	6	45							
															25,73±0,45			0,41±0,02	166,99±2,93	51,54±0,82^(b)	> 14 - adult	Morphotype 5	

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Table 4. Footprints and relative measures used for the Principal Component Analysis. Anatomical abbreviations as in Methods Section.

FOOTPRINTS			LENGTHS							WIDTHS	
ID	IN SITU	CAST 1950-51	Dt1-BL (cm)	Dt2-BL (cm)	Dt3-BL (cm)	Ball medial (mtm-BL) (cm)	Ball lateral (mtl-BL) (cm)	Heel medial (ccm-BL) (cm)	Heel lateral (ctul-BL) (cm)	Ball (mtm-horiz) (cm)	Heel (ctul-horiz) (cm)
SM3	X		13	12,3		10,5	9,2	2,3	2,4	5,5	4,3
SM4	X		13,5	12,5	11,5	10,2	8	2,2	1,6	5,5	4,2
SM43	X		13,5	13,5		10,5	9,4	2,2	1,8	6	4,6
SM17	X		14,2	13,8	13,5	10,2	8,5	2	1,8	6,5	4
SM5	X		17	16,8	15,5	12	12	2,5	2	6,5	5
SM42	X		17	16,8		12,5	11,5	3,4	2,5	7	5,4
SM26	X		18	16,5	15			2	3		5
CA8	X	X	20,2	19,8	19,4	15	13	2,6	2	7,5	4,5
C10	X		20,5		19,2	15,5	12,5	2,8	2,6	7	5,6
SM15	X		20,5	20,5	18,5	15,4	13	4	2	7	6
SM11	X		21	20,2	19,7	15,4	14,5	3,3	2,3	7,5	6
SM6	X		21	21,5	20,5	17,5	15,5	4	2,2	9,2	5,7
SM1	X	X	21,2	21,3	20,8	17,4	14,8	3,8	2,5	8	6
C33	X	X	22,2	21	19,5	15,5	10,7	2,5	2	10	5,8
C36	X	X	22,7	21,7	19,5		14,5	3	2,5		5,5
M21		X		21,6	21,3	16,7	14,6	3,5	2,4	9,6	6,2
CA1	X	X	22,4	21,8	20,8	14,8	12,8	3,1		8	
CA2	X		22,5	22	21	17,3	15,2	3,5	3,5	8,8	6,4
C61	X	X	23	21,7	20,8	16,4	14	3,8	3	7,5	5,4
C63	X	X	23,3	22,2	20,8	17	14	3,5	3,8	8,5	5,3
C60	X	X	25,3	24,2	22,7	18	14,8	3,5	3,3	10,5	6,4
C37	X	X	25,7	23,8	22,5	18,4	14,7	3,7	3,5	10,5	7
C35B	X	X	26,2	24,8	22,8	17	13,7	3,7	2,7	9,5	6,7

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709 **Appendix 1**

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711 **Table A. Scores obtained from the Principal Component Analysis**

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ID	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
SM3	-0.39913	0.10426	-0.064014	0.014386	-0.025072	0.016054	0.016716	0.011934	0.0074328
SM4	-0.50068	-0.042109	-0.014907	0.032287	0.0032614	-0.029028	0.019643	-0.026998	0.0033618
SM43	-0.40104	-0.019701	-0.0054895	0.018735	0.0016977	0.027812	-0.0033284	0.0083841	-0.0075861
SM17	-0.42507	-0.0052715	0.061746	0.0063252	-0.038382	-0.016919	-0.0164	0.0059965	-0.0012712
SM5	-0.1976	-0.035523	-0.0043672	-0.03242	0.024328	0.032498	-0.025789	-0.011295	-0.0026746
SM42	-0.086943	0.013761	-0.08784	0.050378	-0.009608	-0.0043334	-0.025838	0.015148	0.0033864
SM26	-0.20626	0.16623	0.063691	-0.021075	0.045203	0.0078808	-6.97E-02	-0.013948	-0.00040047
CA8	-0.051293	-0.079409	0.054639	-0.097538	-0.026619	-0.014175	-0.002064	0.014186	0.00038865
C10	0.0058167	0.019522	0.0058477	-0.035311	0.03647	-0.00018801	0.032056	0.019886	0.0034661
SM15	0.040758	-0.12904	-0.095157	0.017228	0.043206	-0.034662	0.00082729	-0.005932	-0.0085001
SM11	0.06668	-0.064129	-0.032745	-0.023447	0.034482	0.026778	-0.0049565	0.0063519	0.0068743
SM6	0.15624	-0.12859	-0.045021	0.0020611	-0.050337	0.019214	0.001418	-0.0080637	-0.0071906
SM1	0.14791	-0.061674	-0.059992	-0.0097849	0.00034344	0.0088016	0.019386	0.010087	-0.0078662
C33	0.0099173	-0.09178	0.16838	0.043167	0.0021726	-0.017624	0.012848	0.010468	-0.0049062
C36	0.094929	-0.029812	0.032258	-0.047049	0.0025717	0.013716	-0.009842	-0.02199	0.0015418
M21	0.16838	-0.0796	0.021892	0.019189	-0.011351	0.022302	-0.0073946	0.0015577	0.014584
CA1	0.16391	0.21771	-0.0025937	0.0040729	0.0067048	-0.016137	-0.017977	0.012136	-0.0084853
CA2	0.22089	0.072731	-0.022013	0.006969	-0.0012392	0.036927	0.012619	-0.0038898	-0.0063643
C61	0.15271	0.023445	-0.066418	-0.034022	-0.0050802	-0.045788	-0.0011026	-0.0017506	0.007746
C63	0.19883	0.1176	-0.020327	-0.025171	-0.043065	-0.029182	0.0070871	-0.013733	-0.00144
C60	0.28381	0.030453	0.049268	0.0231	-0.021083	0.01058	-0.0018458	-0.0051978	-0.00067736
C37	0.3109	0.046052	0.029704	0.054401	-0.0019844	0.016719	0.011316	-0.0085163	0.0054307
C35B	0.24634	-0.045122	0.033459	0.033518	0.033381	-0.031244	-0.01731	0.0051775	0.0031501

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715 **Table B. Loadings for each principal components. a, Dt1-BL; b, Dt2-BL; c, Dt3-BL; d, Ball medial (mtm-BL); e, Ball lateral (mtl-BL); f, Heel medial (ccm-BL); g,**
 716 **Heel lateral (ctul-BL); h, Ball (mtm-horiz); i, Heel (ctul-horiz).** Anatomical abbreviations as in Methods section.

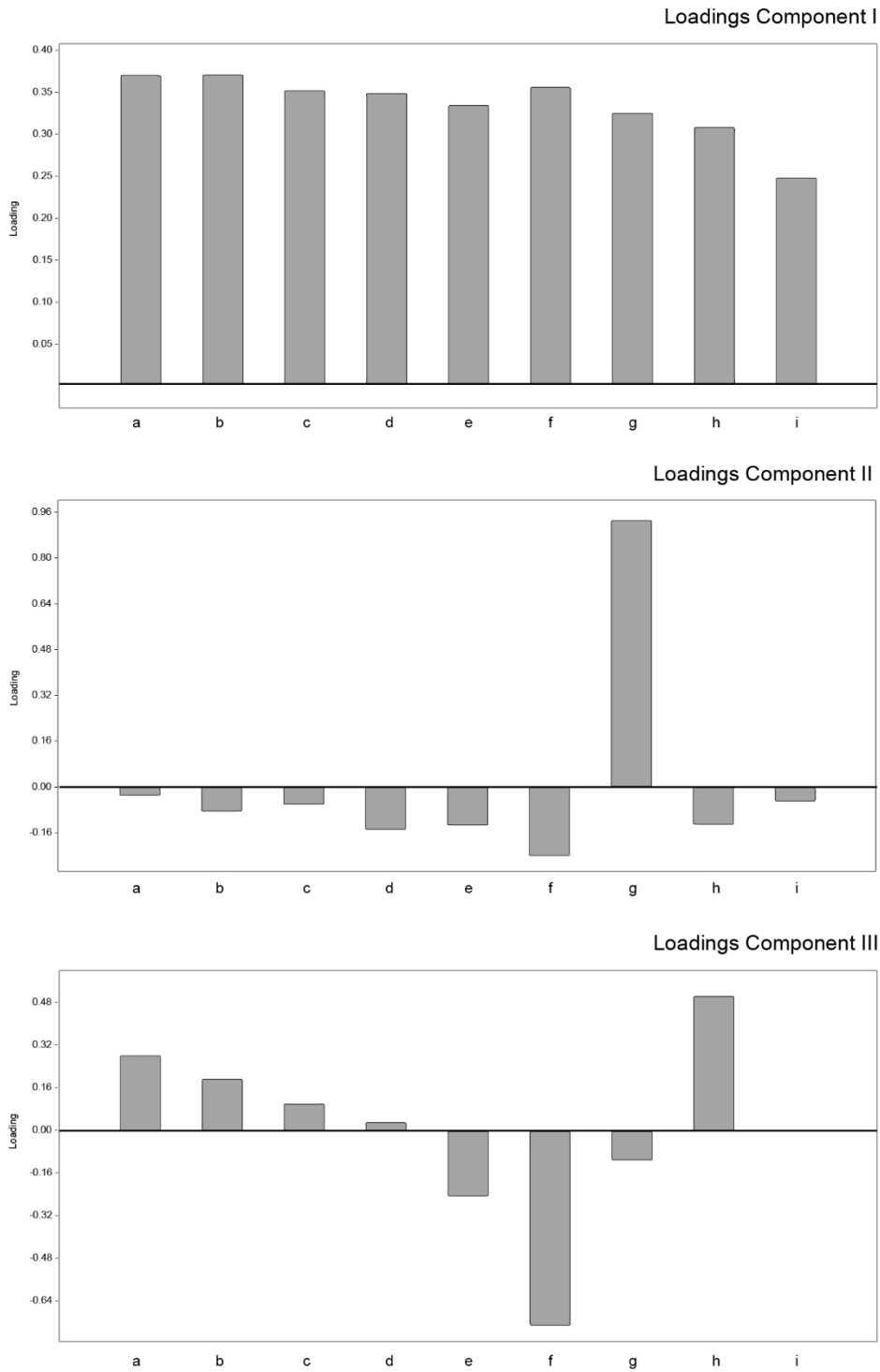
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	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
a	0.36632	-0.031724	0.28459	-0.15437	0.31322	-0.38384	-0.061146	-0.3656	0.61412
b	0.36721	-0.086634	0.19468	-0.1893	0.19705	-0.27853	-0.3069	-0.13269	-0.74546
c	0.34834	-0.062518	0.10263	-0.17626	-0.035551	-0.093333	-0.12422	0.88253	0.16995
d	0.34521	-0.15	0.03307	-0.16341	-0.13051	-0.019176	0.88858	-0.036893	-0.14898
e	0.33106	-0.13532	-0.24619	-0.50577	-0.065819	0.67412	-0.2218	-0.19439	0.099588
f	0.35243	-0.24194	-0.73379	0.3425	-0.19673	-0.31842	-0.1176	-0.070489	0.051056
g	0.32186	0.93175	-0.1145	0.050472	-0.09853	0.019641	0.025317	-0.030012	-0.030921
h	0.30501	-0.13213	0.50725	0.46978	-0.57082	0.21548	-0.15222	-0.12269	0.031883
i	0.245	-0.051134	-0.0026745	0.53499	0.68278	0.40417	0.10113	0.098963	-0.039702

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Figure 5-figure supplement 1. Loadings for the first three principal components. a, Dt1-BL; b, Dt2-BL; c, Dt3-BL; d, Ball medial (mtm-BL); e, Ball lateral (mtl-BL); f, Heel medial (ccm-BL); g, Heel lateral (ctul-BL); h, Ball (mtm-horiz); i, Heel (ctul-horiz). Anatomical abbreviations as in Methods section



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730 Additional files

731

732 Supplementary File 1.

733 Supplementary table with all the tracks analyzed in the study.

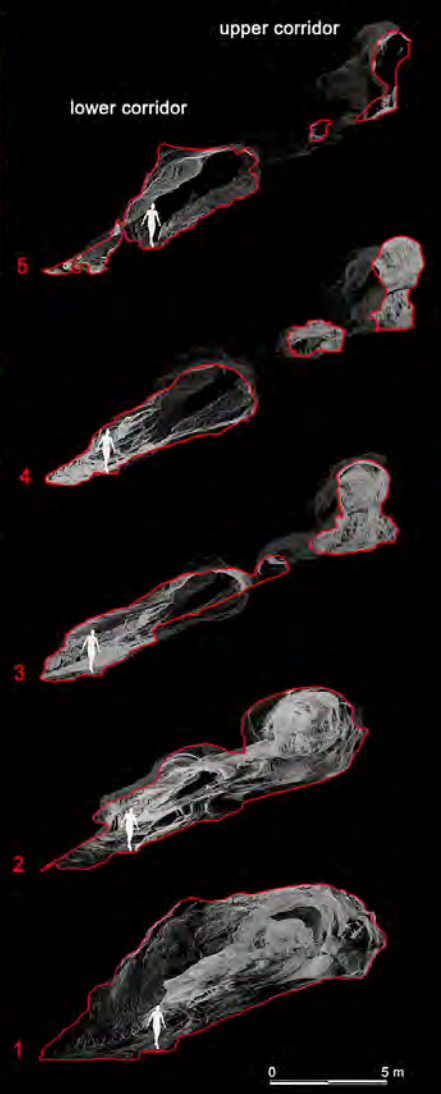
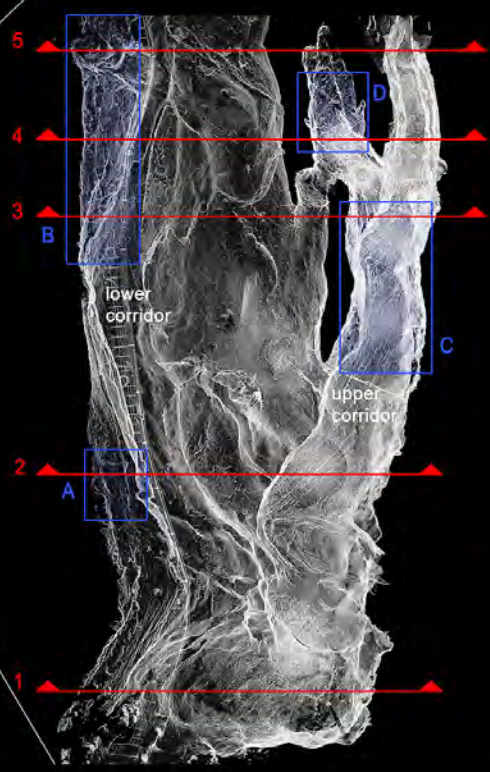
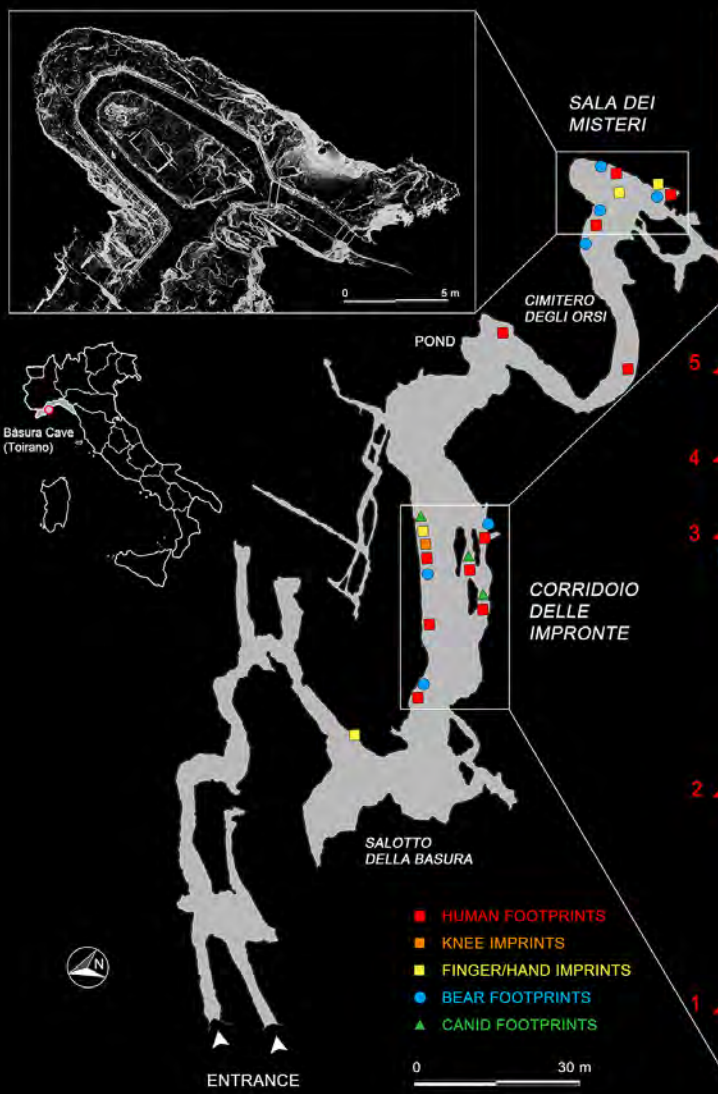
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735 Video 1

736 Virtual exploration of the cave showing the crawling locomotion adopted by the Palaeolithic group to cross
737 the main gallery and to access the innermost rooms of the cave .

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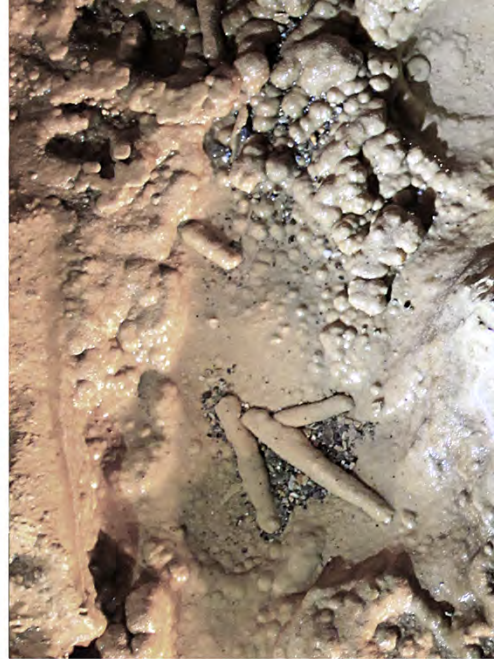




C37



CA1



C9



C33



SM15



CA8



SM5



SM42



SM17 - SM18



C0



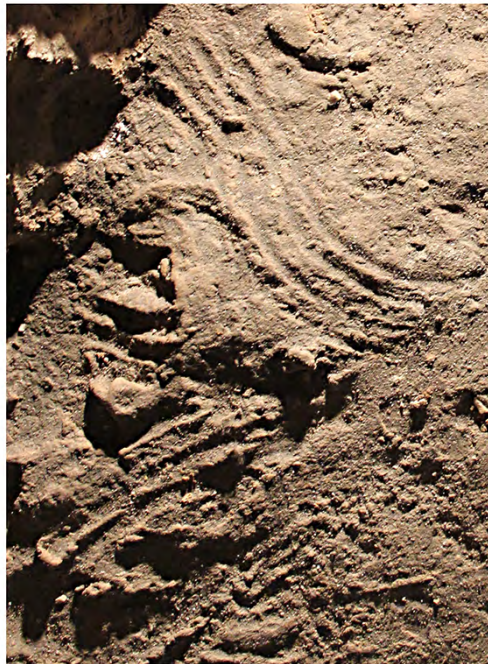
C26b



C72



SM44



SM55



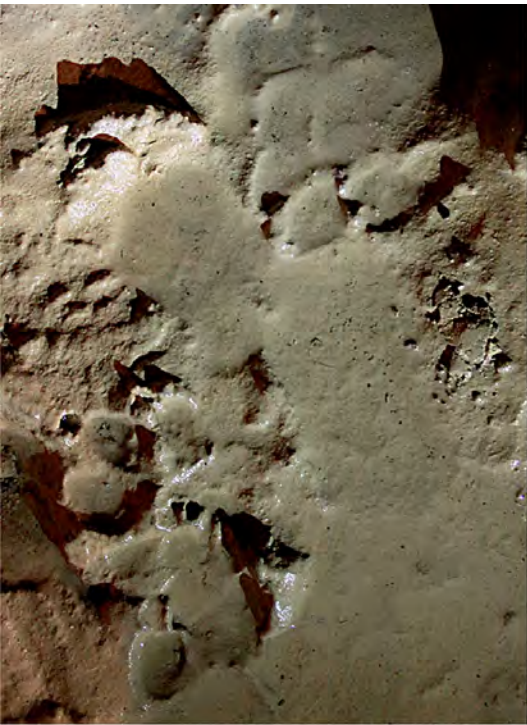
SM56



P8.1



P1.6



C47 - C48 - C53



CA12



C17 - C67



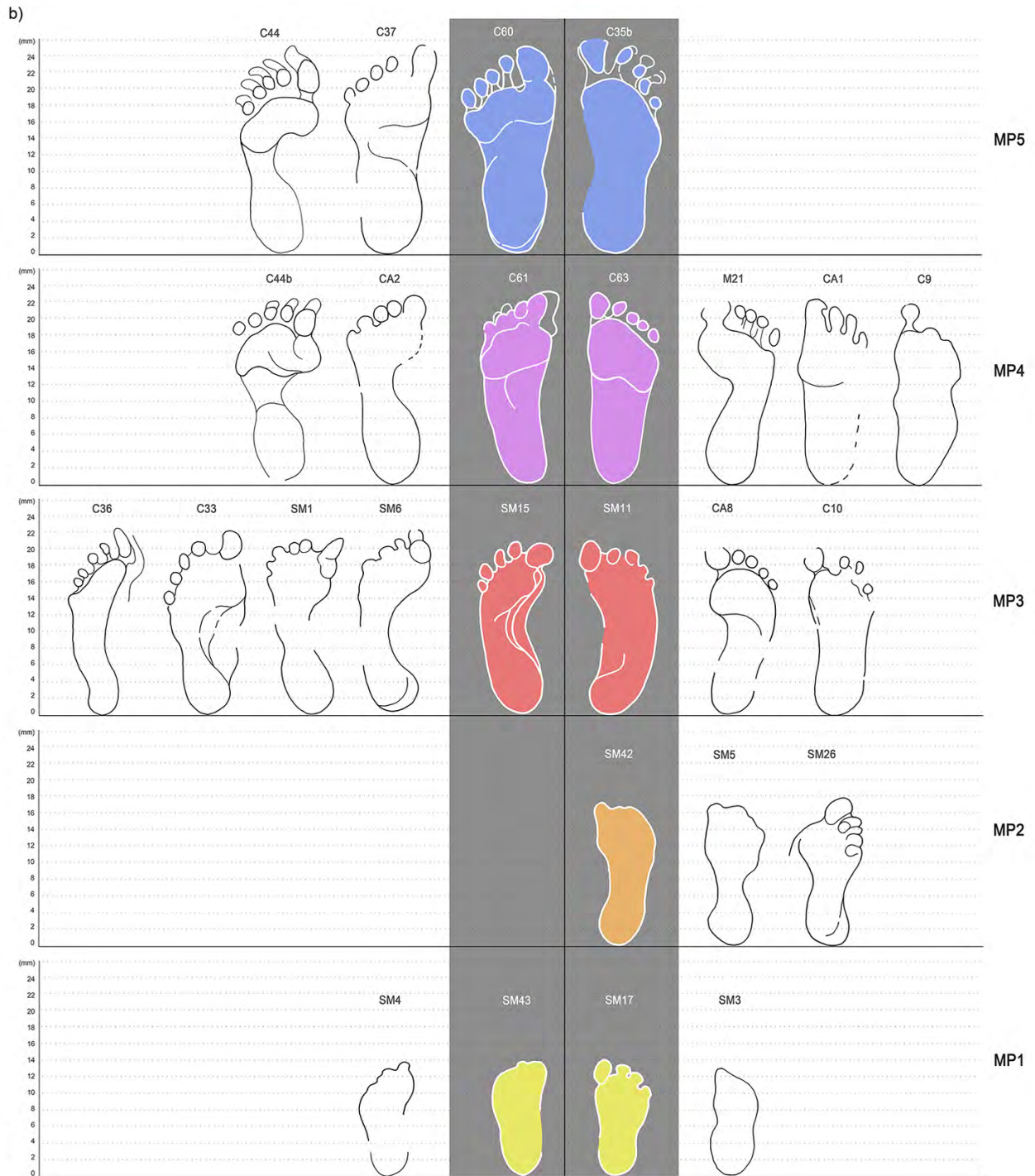
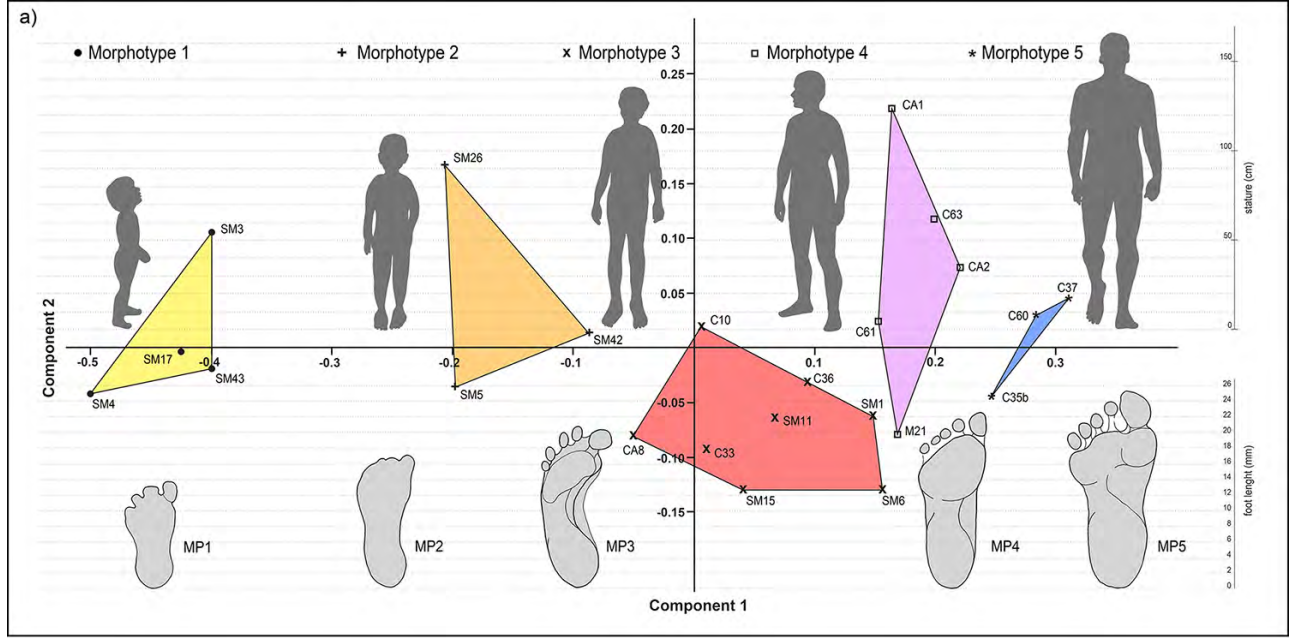
SM12

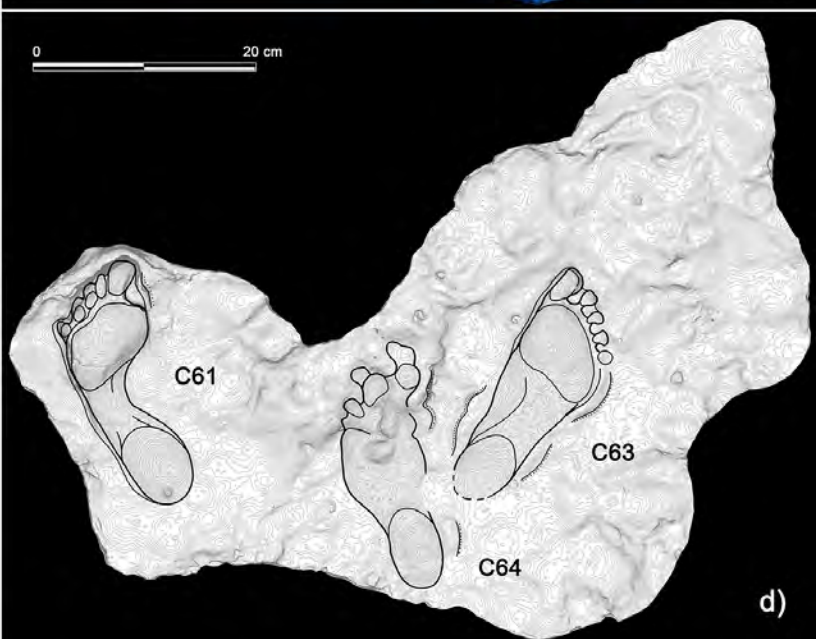
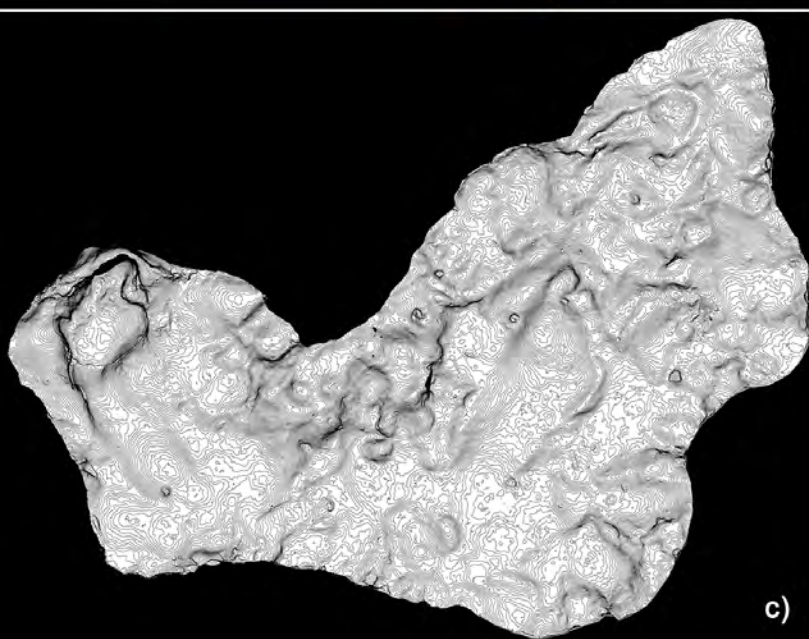
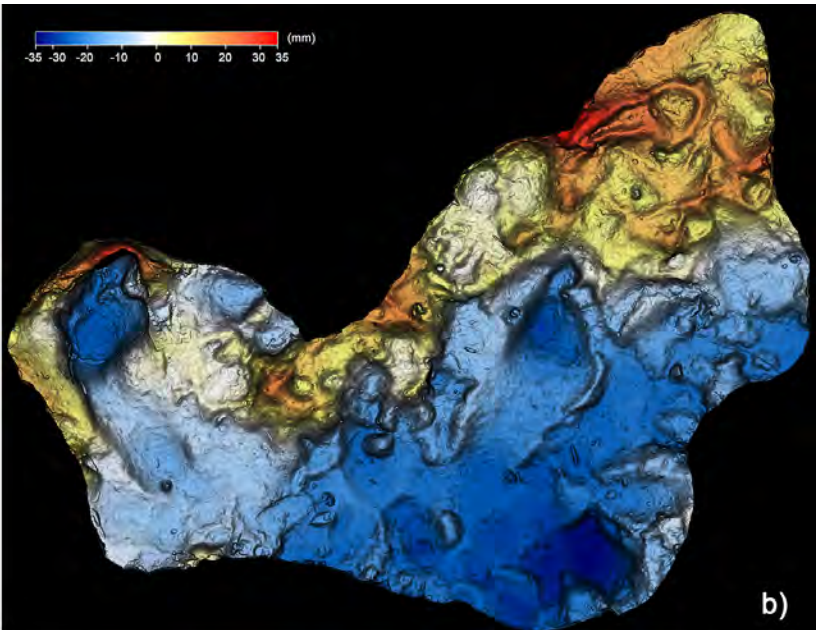


SM41



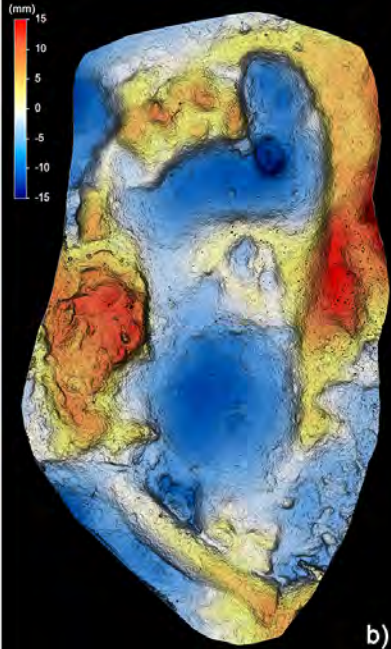
C12







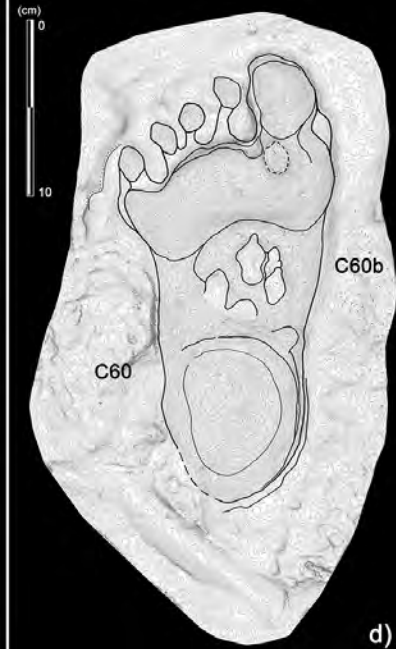
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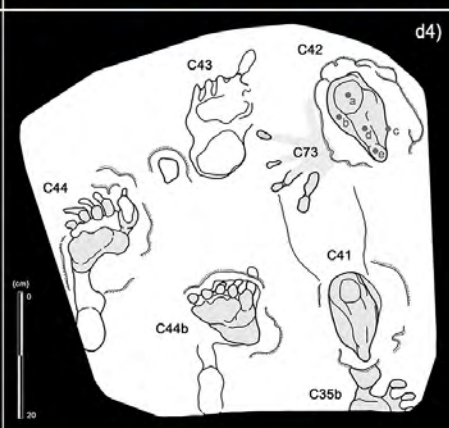
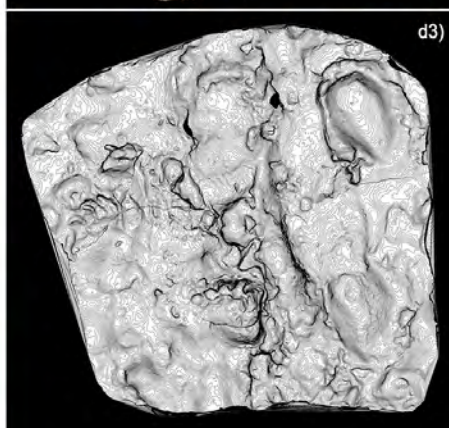
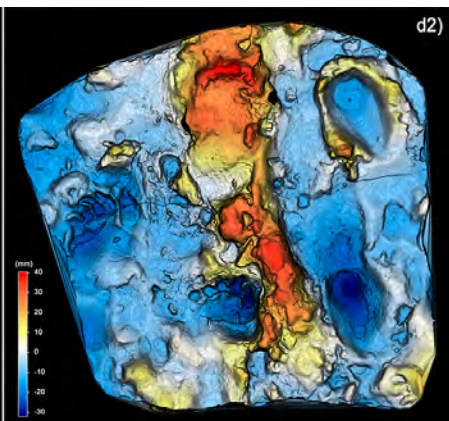
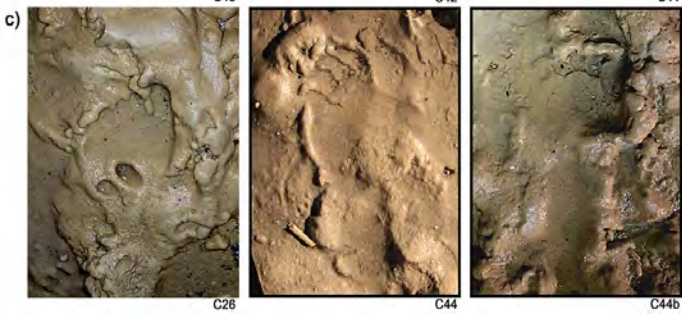
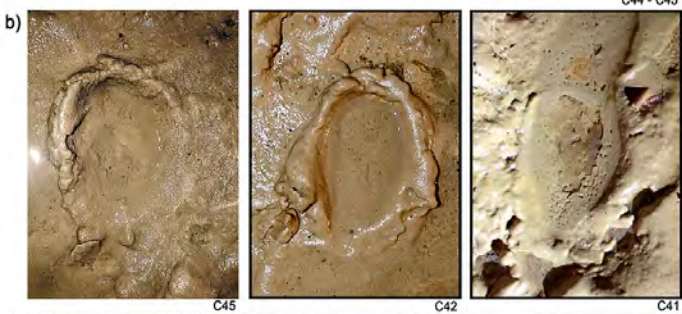
b)

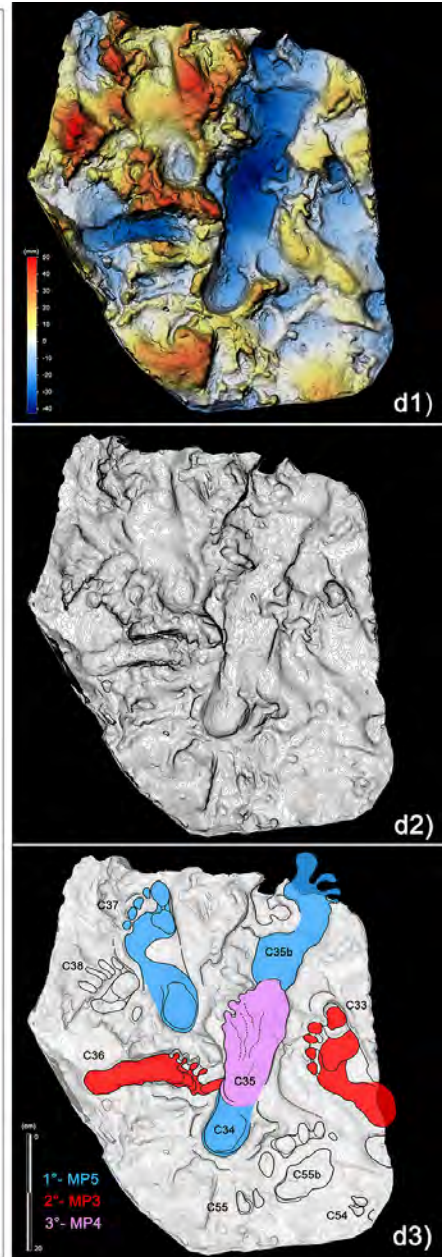
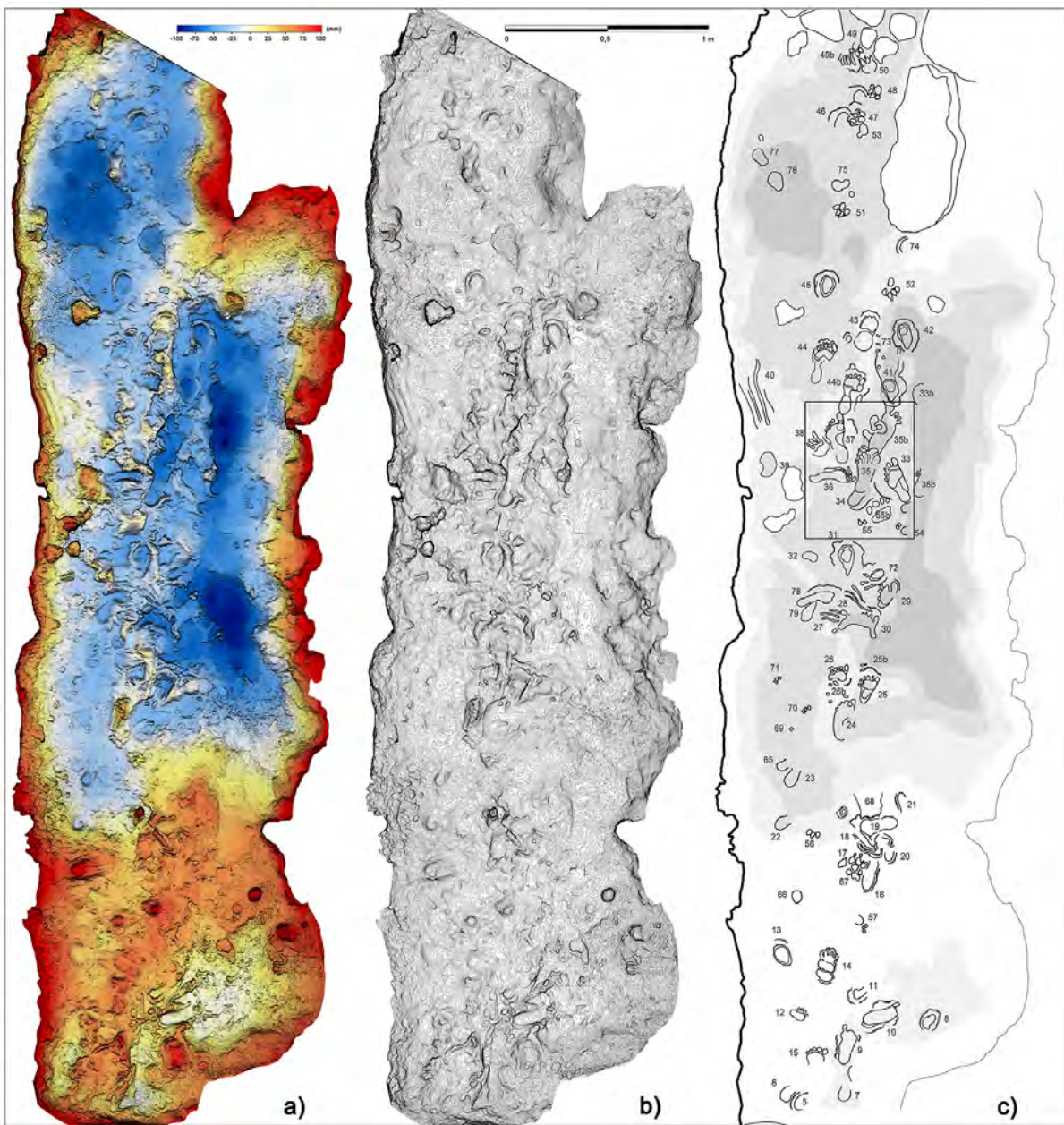


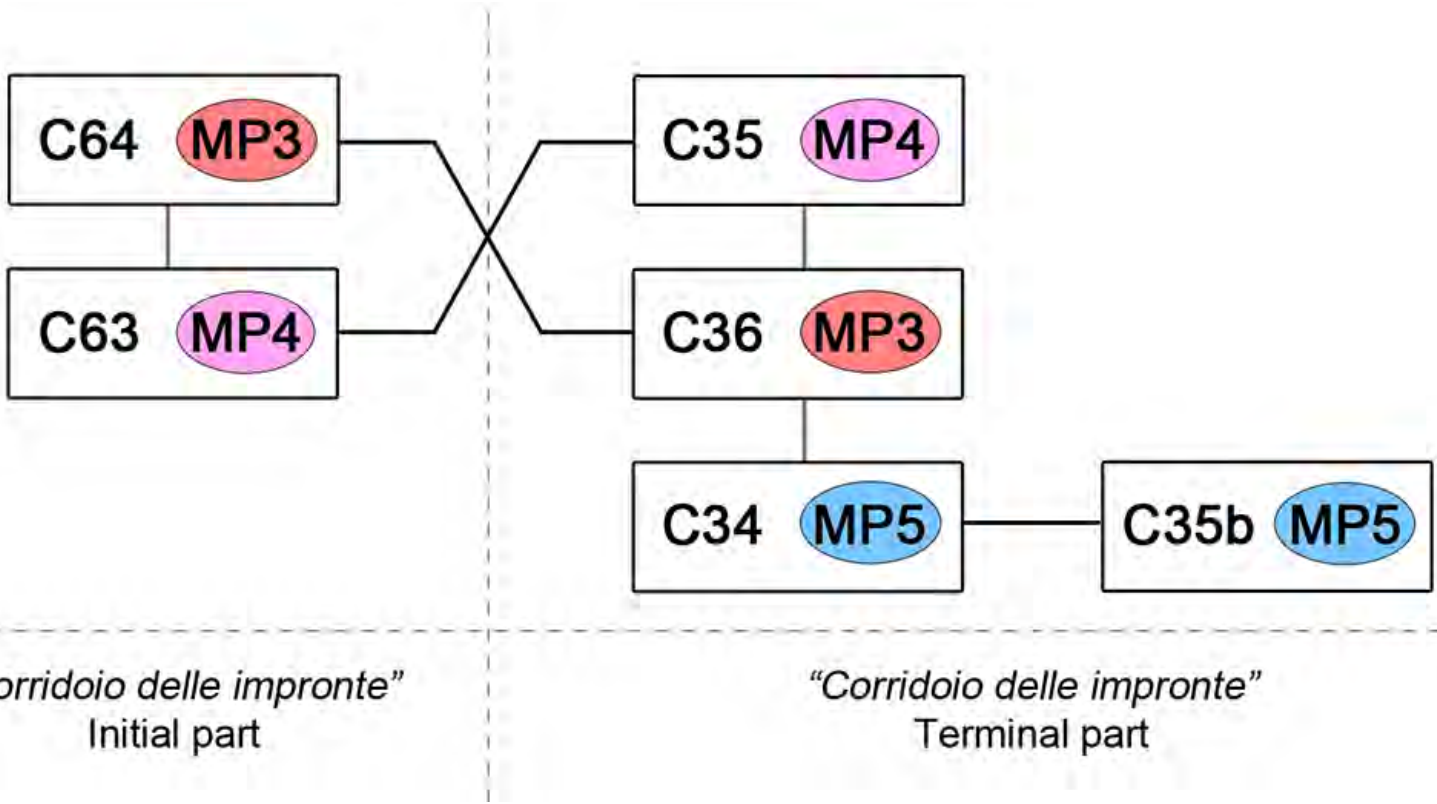
c)



d)





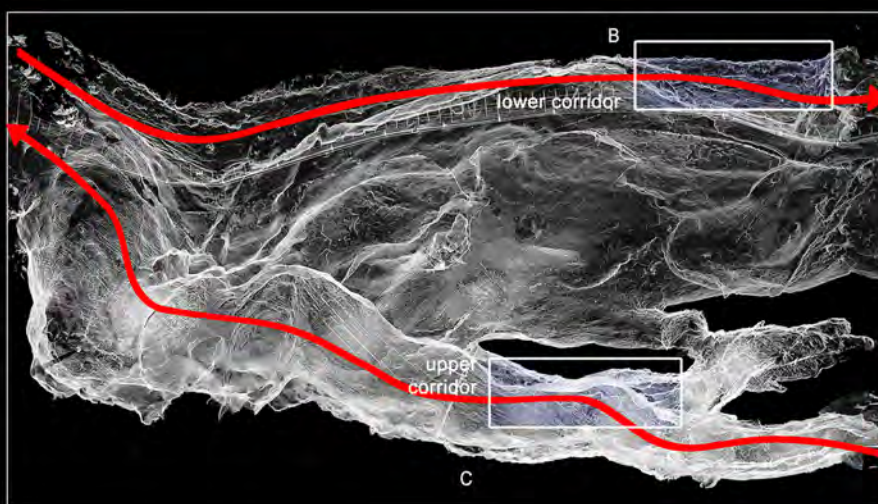


B - Lower corridor

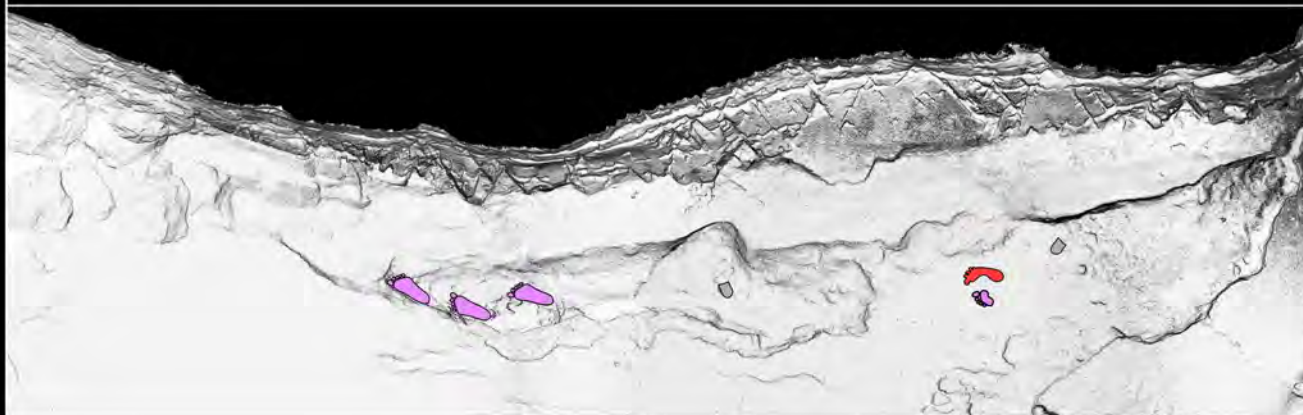


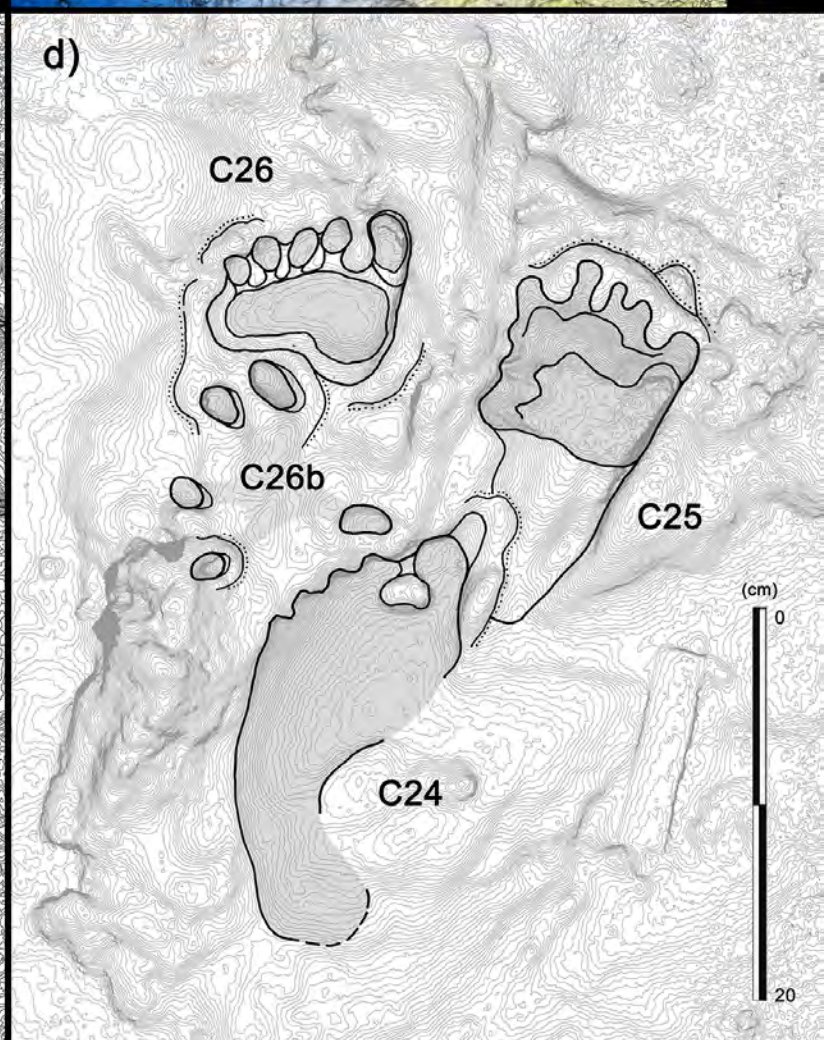
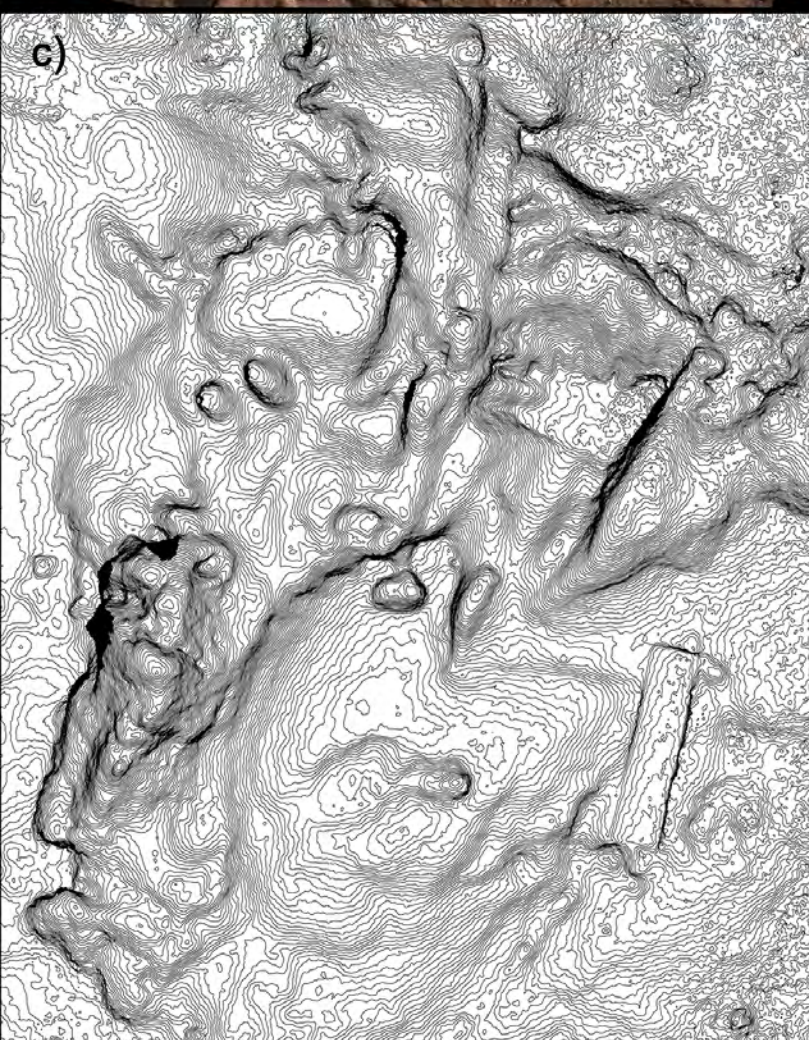
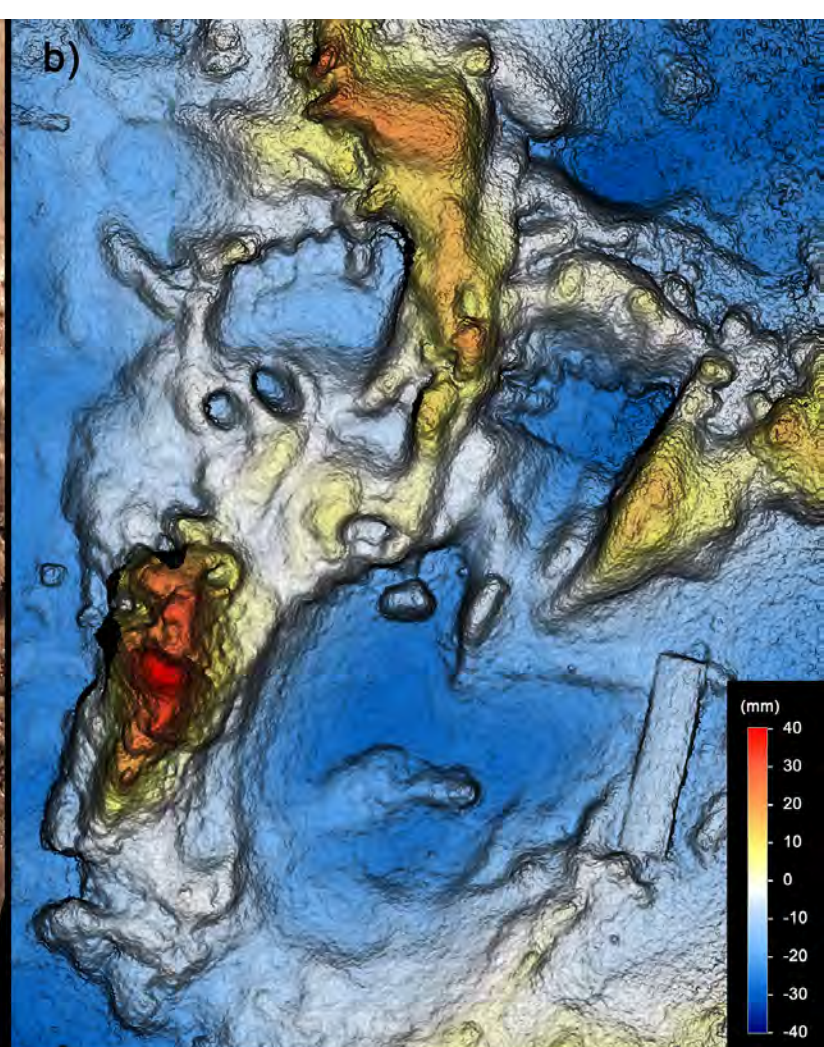
- COMPLETE FOOTPRINT
- HEEL IMPRINT
- FOREFOOT IMPRINT
- KNEE IMPRINT
- FINGER/HAND IMPRINT
- MORPHOTYPE 3
- MORPHOTYPE 4
- MORPHOTYPE 5
- UNCERTAIN

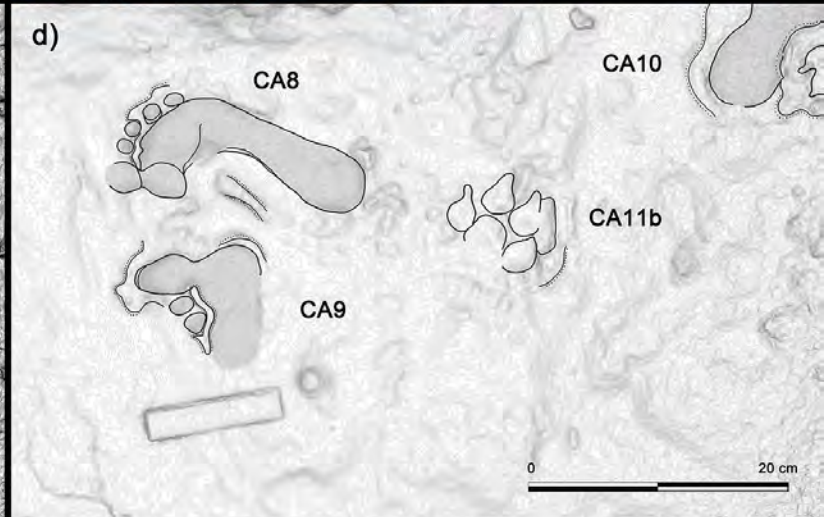
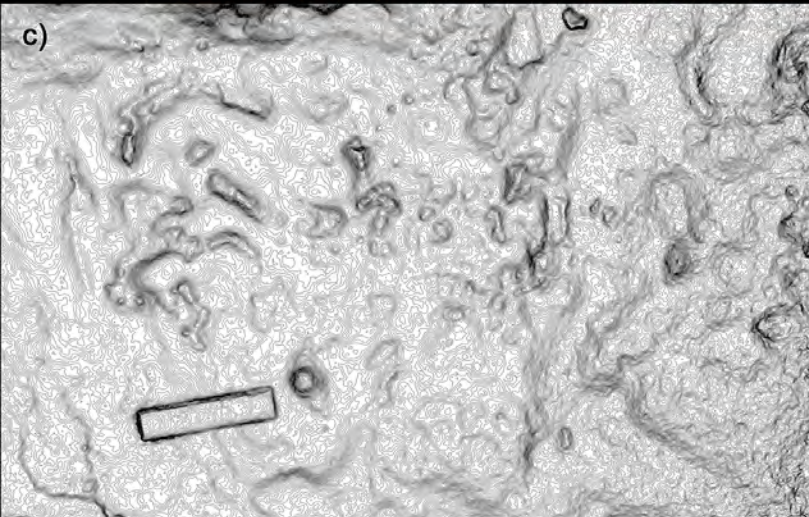
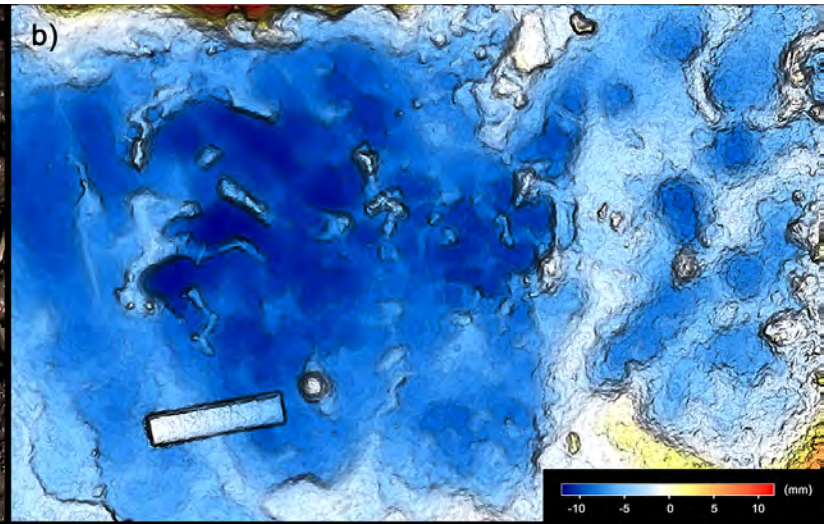
ENTRANCE

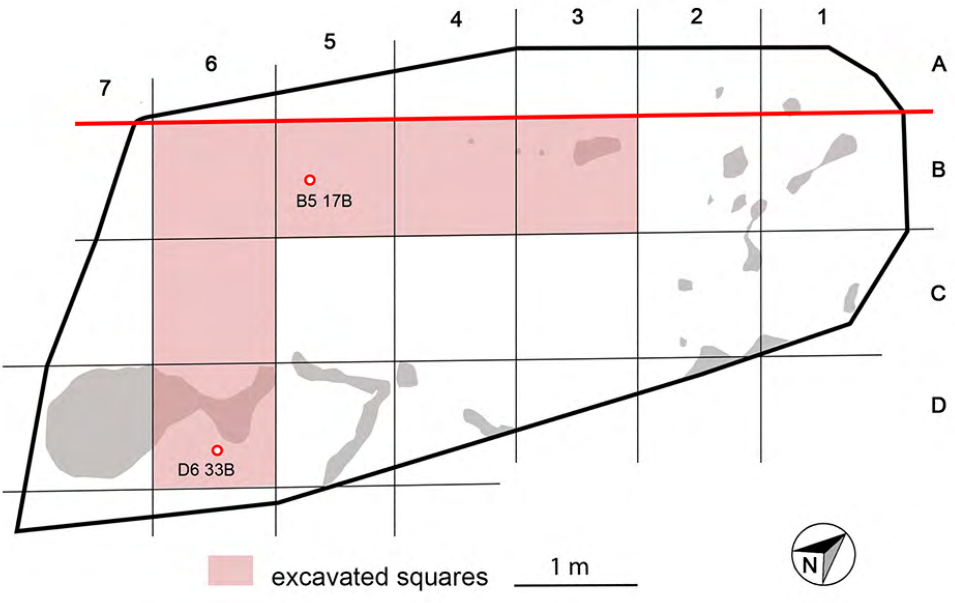
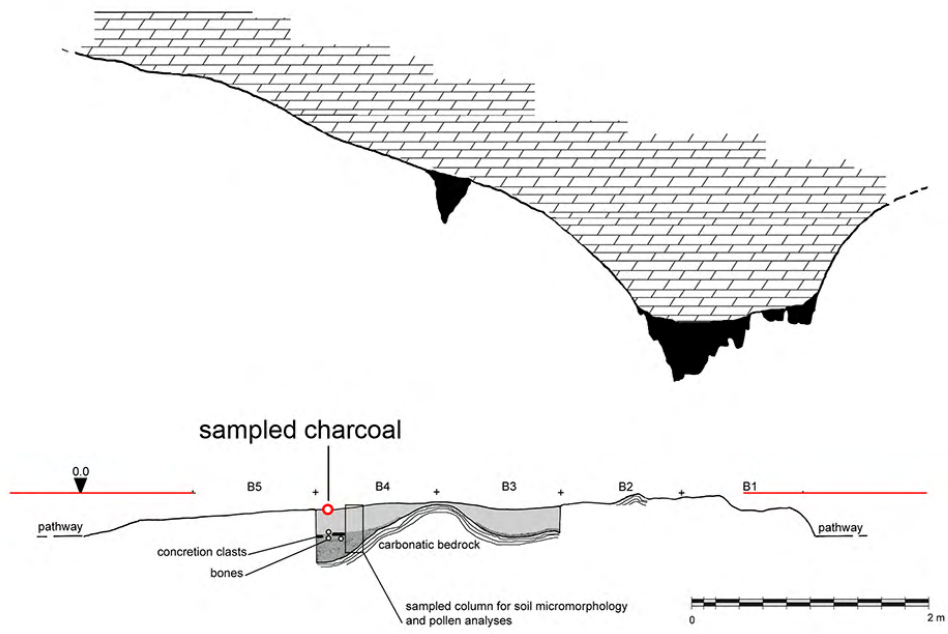


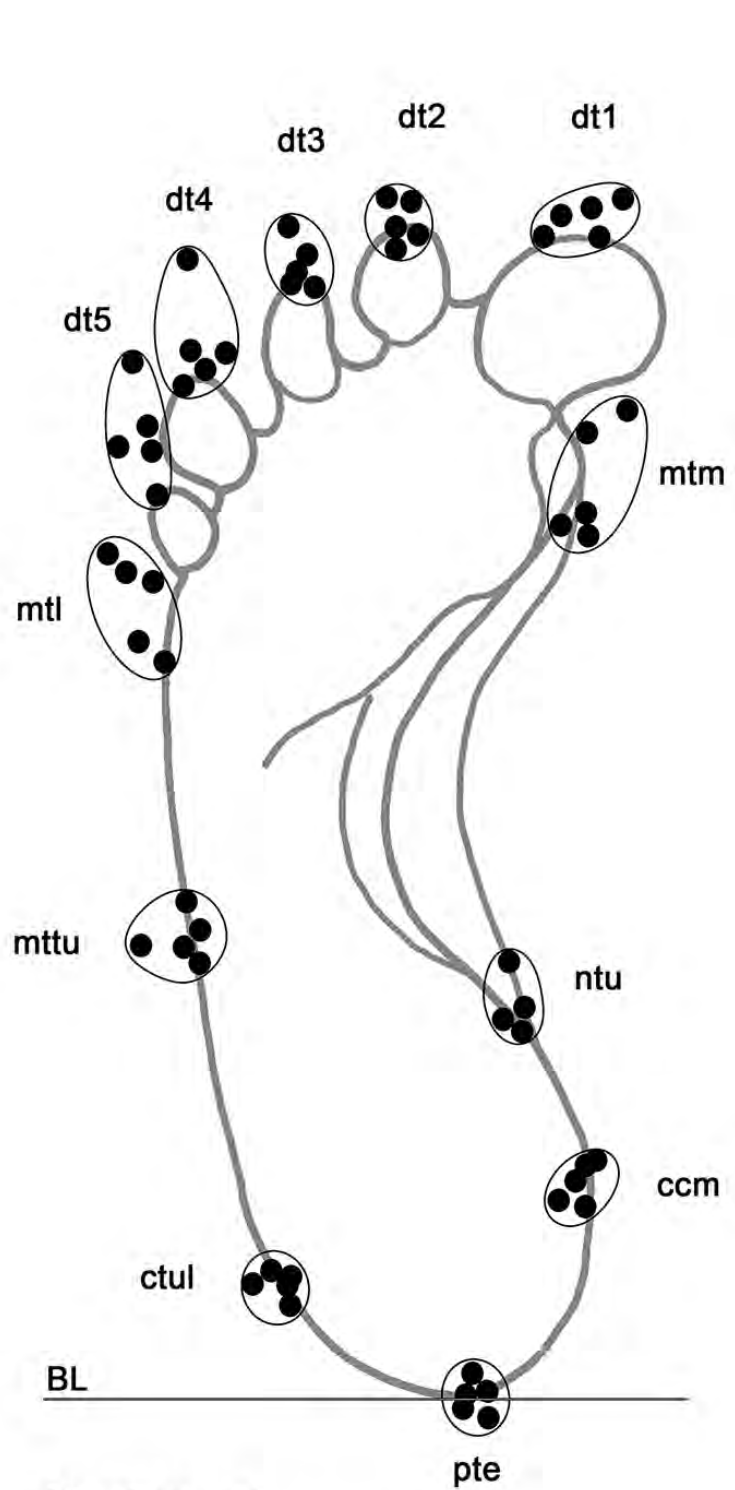
C - Upper corridor



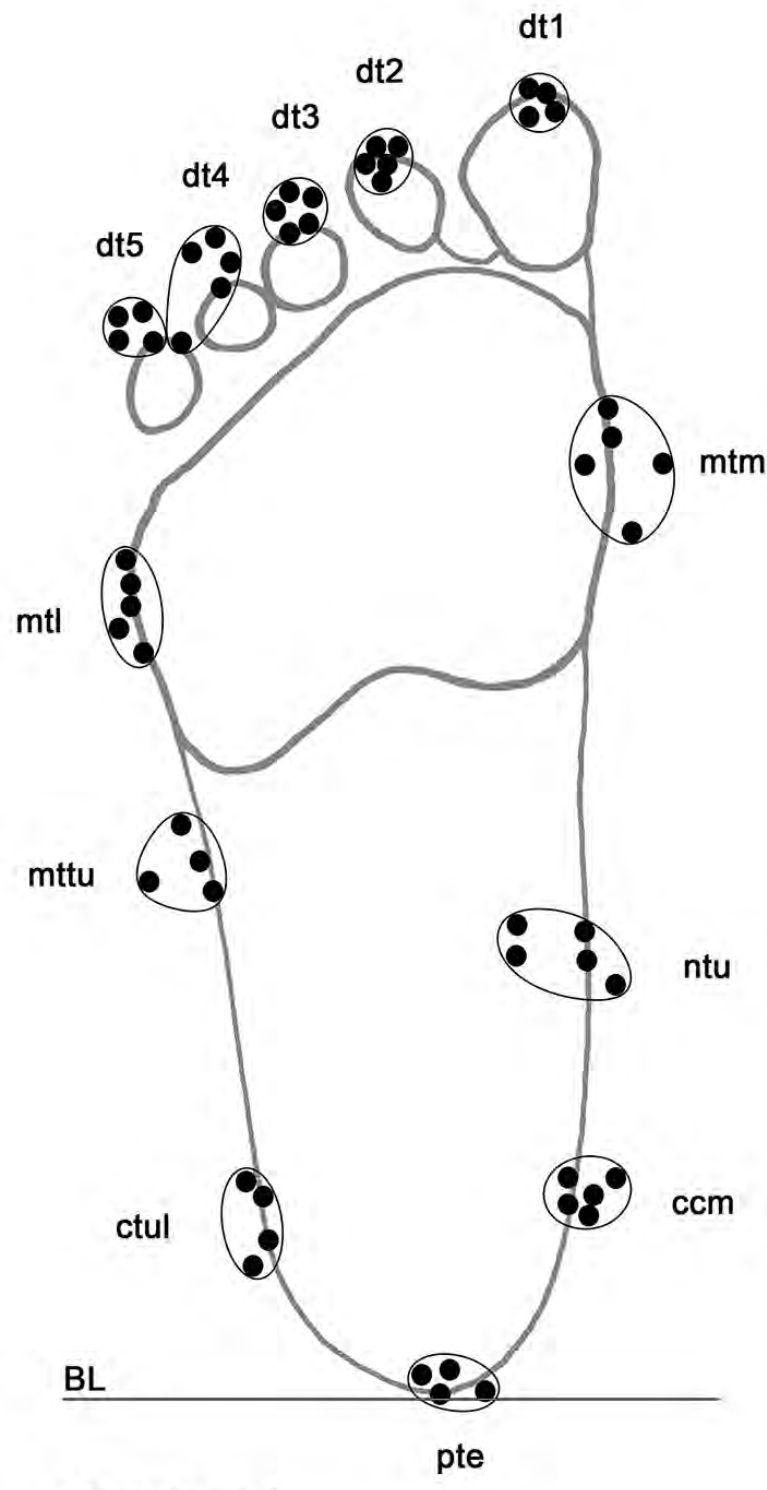






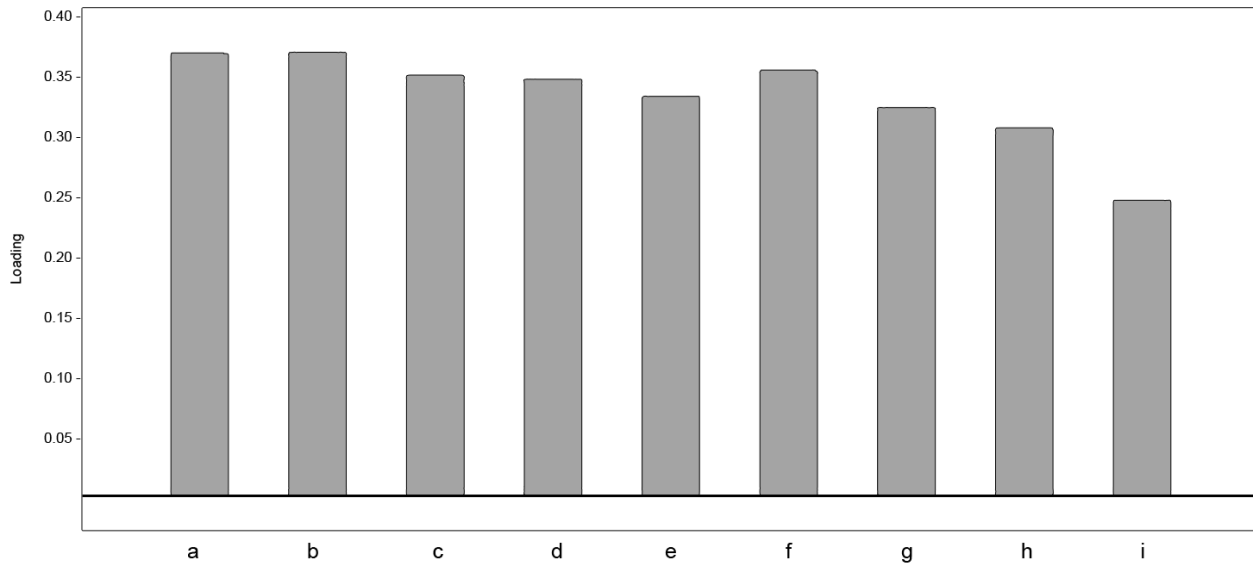


Morphotype 3

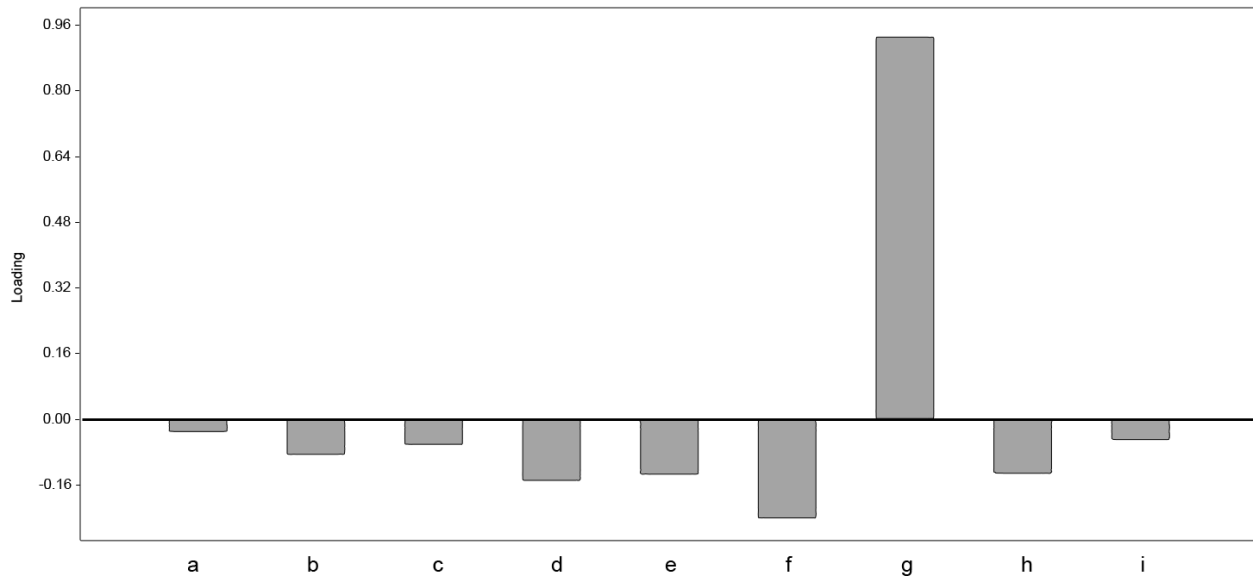


Morphotype 4

Loadings Component I



Loadings Component II



Loadings Component III

