Biological Sciences: Anthropology/Evolution

Late Neandertals in Southeastern Iberia:

Sima de las Palomas del Cabezo Gordo, Murcia, Spain

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Manuscript pages:
Tables: 0
Figures: 8
Abstract word count: 110
Character count:

Abbreviations: SP: Sima de las Palomas; MIS: marine isotope stage; GIS: Greenland Interstadial; ^{14}C BP: radiocarbon years before present; cal BP: calendar years before present; MPMH: Middle Paleolithic modern humans; EUP: Early Upper Paleolithic; MUP: Middle Upper Paleolithic; OSL: opticaly stimulated luminescence

Abstract Middle Paleolithic fossil human remains from the Sima de las Palomas in southeastern Iberia, dated to ≤43,000 – 40,000 cal BP) present a suite of derived Neandertal and/or retained ancestral morphological features, in the mandibular symphysis, mandibular ramus, dental occlusal morphology, and distal hand phalanx. These traits are combined with variation in the mandibular corpus, discrete dental morphology, tooth root lengths, and anterior dental size that indicate a frequency difference with earlier Iberian and more northern European Neandertals. The Palomas Neandertals therefore confirm the late presence of Neandertals associated with the Iberian persistence of the Middle Paleolithic, but suggest microevolutionary processes and/or populational contact with contemporaneous modern humans to the north.

Key Words: Middle Paleolithic, Mandible, Dentition, Postcrania

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It has become apparent that the transition from a Europe populated by Neandertals to one occupied by early modern humans during marine (oxygen) isotope stage (MIS) 3 consisted of a westward spread of modern humans, variably absorbing at least some local Neandertal populations (1,2). However, the detailed aspects of this population process remain obscure as a result of the scarcity of well-dated late Neandertals and early modern humans, despite the recent direct dating of several specimens from both samples (3-9). If we are to understand the paleobiogeography of this process, and hence the potential patterns of interactions between these two morphologically defined human groups, then it is essential to document the biology of both the earliest modern humans and the latest Neandertals.

It has been recognized for some time that the Middle Paleolithic, generally presumed in Europe to have been the product of Neandertals, persisted substantially longer in Iberia south of

the Pyrenees (south of the "Ebro Frontier") than elsewhere in Europe, to ≈34,000 (≈34 ka) cal BP (≈30 ka ^{14}C BP) (10; supporting information (SI) Fig. 1). Even though there are Iberian Neandertal remains which have been referred to this age (11), their purported late age has been placed in doubt (12). At present, the most recent, securely dated, diagnostic Neandertal fossil from the region is the Oliveira 1 middle manual phalanx at ≈43,500 cal BP (≈39 ka ^{14}C BP) (13), about the same age as the northern Spain El Sidrón remains (7). It is in this context that we present a series of Neandertal remains from the upper levels of the Sima de la Palomas in southeastern Spain.

Context of the Palomas Human Remains

The Sima de la Palomas Sima de las Palomas (Rock-Dove Hole) is a karstic shaft (37° 47' 59" N, 0° 53' 45" W) in the Permo-Triassic marble of a hill (Cabezo Gordo) in Torre Pacheco township, Murcia, reaching 312 m a.s.l., overlooking the Mar Menor coastal lagoon of the Mediterranean Sea [SI Figs. 1 and 2]. The main shaft is 18 m deep, opening beneath overhanging rock at ~123 m a.s.l. (SI Figs. 3 and 4). The shaft´s brecciated contents were largely emptied by 19th century miners, who left a sediment column down one side and scattered fossiliferous rubble on the hillside. Systematic collection of disturbed remains and excavation of the upper breccia deposits were begun by MJW and the late J. Gibert following discovery of a crushed facial skeleton (Palomas 1) from the uppermost breccia by J. C. Blanco in 1991 (14,15). Excavation is continuing in the uppermost 2–3 m, the Upper Cutting, directed by MJW and MVL. Fossil human remains have been collected from the mine rubble (1992-99) and excavated *in situ* (1994-present) (SI Table 1).

A number of the *in situ* human remains come from above, within, and slightly below a fusiform lens of dark-gray sediment (burnt, according to x-ray diffraction and fluorescence analyses). It attained a maximum thickness of ≈20 cm in the angle of an 'L' shaped excavation area in the Upper Cutting, covering a thin, oblong marble slab (≈40 x 30 x 10 cm) between levels 2k and 2m). The lens petered out, both near the open shaft and below the entrance where it covered part of the foot of a downward and inwardly steeply-sloping (30°-40°) éboulis or scree of marble blocks ≤50 kg. A more consistent and widespread lower layer of dark-gray sediment lies beneath level 2l, fading away beside the open shaft (Fig. 1; SI Figs. 5 & 6).

Only human bones and teeth from sediments postdating the éboulis (from levels no deeper than 2l) are dealt with here. Although these later sediments contain few large rocks and were laid down horizontally, they often have a coarse texture implying that they were washed from the hillside into the cave and down the steep interior scree slope; the slope had developed neither an eroded surface nor a calcrete crust, in contrast to the thin calcite deposit on the hillside which eventually sealed off the éboulis. These later sediments contained Middle Paleolithic artifacts, animal bones (some of which are burnt), and pollen indicative of mild climatic conditions (14,16,17). Due to carbonate precipitation, the éboulis is in part cemented into irregular brecciated conglomerate masses, in which there are Middle Paleolithic artifacts, faunal remains, and variably articulated and crushed human remains. The human fossils include the Palomas 92 and 96 partial skeletons, the Palomas 93 to 95 teeth, and the remains of at least two more individuals including crania with mandibles; these fossils are currently under preparation and analysis, and they will be dealt with in the future.

Chronological Age of the Palomas Human Remains The age of the human fossils of concern here is primary, since the issue is the morphology of the latest Neandertals in Europe. The Palomas artifacts are all Middle Paleolithic, made on retouched flakes of flint, quartz, rock crystal, and marble (14-16,18). Given current reliable dates for Iberian Middle Paleolithic assemblages (10,19), this indicates an age of ≥34 ka cal BP (≥30 ka ^{14}C BP) for the deposits.

Collagen preservation is poor in the Palomas human remains, and direct ^{14}C dating of the human bones has not been possible. However, a combination of dating techniques permits chronological control of the Upper Cutting (see SI Figs. 7 and 8 for the stratigraphic positions of the samples).

A burnt faunal bone directly adhering to the Palomas 59 mandible in level 2f provided a date of 34,450 ± 600 ^{14}C BP (OxA-10666) (95% CI: 40,950 – 37,622 cal BP using the Cariaco06 ^{14}C curve (20)). A burnt lagomorph bone from the deeper level 2l provided a statistically identical age of 35,030 ± 270 ^{14}C BP (OxA-15423) (95% CI: 40,986 – 38,850 cal BP). Given the natures of the dating specimens and the moderately high C:N atomic ratios for these samples (albeit an expected elevation given the burning), it is likely that these ages fall closer to the upper limits of the 95% confidence intervals for these dates (SI Section III). This interpretation of these dates from the upper sediment fill is supported by the associated palynology (17), which shows relatively temperate conditions, probably during GIS9 and therefore slightly before the onset of the severely cold Heinrich 4 oscillation ≈40 ka cal BP (21).

To assess further the ages of these deposits and the stratigraphically older éboulis deposits, U-series (LA-ICP-MS) dates were obtained from three bones (SI Section IV). A date of 43,800 ± 750 cal BP (APSLP4) is from a faunal specimen from level 2i; it is slightly earlier than the likely ^{14}C calibrated ranges from levels 2f and 2l. Two much older and stastistically similar

U-series dates come from the stratigraphically deeper, steeply-sloping éboulis, one on a Palomas 96 metacarpal from level 2e of 54,000 ± 3,850 cal BP (APSLP1) and the other on a faunal bone from level 2l of 51,000 ± 1,250 cal BP (APSLP6). These U-series estimates presume that the samples were closed systems, which cannot be verified. They should threrefore be regarded only as corroborating the ^{14}C and paleoclimatological assessments of the age of the upper sediment fill and the earlier age of the éboulis level, including some mixed material in the burnt dark-gray sediment horizon.

In addition, a sediment sample (X2509) from the top of level 2k directly overlying the marble slab and hence below the dark-gray sediment level in the northeastern corner of the Upper Cutting was dating using optically stimulated luminescence (OSL) (SI Section V). The sample provided an age estimate of 54,700 ± 4,700 cal BP for these sediments. This determination increases confidence in the U-series dates for stratigraphically similar specimens and hence in the age of the stratigraphically younger deposits dated by ^{14}C.

These dating assessments therefore combine to indicate an age for the upper sediment fill ≈40 ka cal BP but possibly slightly older (*i.e.*, ≈43 ka cal BP). The subsample of the Palomas human remains from this portion of the sediment includes 63 elements, 54 or 85.7% of which are isolated teeth or tooth fragments. They make these Palomas Neandertals the most recent, and largest, sample of southern Iberian late Neandertals currently known. The other Neandertals close in age are the Initial Upper Paleolithic ones from Spy (9), and probably Saint-Césaire, Arcy-Renne and Vindija G_1 (22-24). These Palomas fossils are also approximately the same age as the earliest modern humans in Europe (4,25), albeit at the other end of Europe. If the earliest phases of the Aurignacian were indeed made by modern humans (26,27), then the Palomas remains should overlap in time with modern humans as close as the northern Pyrenees (10).

The Palomas Human Remains

The Palomas fossil human remains therefore consist of three samples. There are the undated and isolated remains discovered in the miners' rubble. There are the partial face, partial skeletons, and isolated remains from the brecciated éboulis. And there are the 63 isolated remains from the excavated deposits at or above the levels dated to ≈40-43 ka cal BP.

The diagnostic remains from the first two samples can all be attributed to Late Pleistocene Neandertals. For the remains out of context, the relevant aspects include supraorbital torus presence (Palomas 11, 12 and 62), retreating mandibular symphyses and lateral corpus thickness (Palomas 6 and 23), incisor and molar occlusal morphology and incisor root length (Palomas 24 and 50), manual middle phalanx breadth (Palomas 65), and femoral diaphyseal shape (Palomas 52). For the brecciated remains, the isolated teeth appear undiagnostic, and Palomas 96 and the other associated skeletons are still largely in breccia. Yet, the Palomas 1 mandible has a retreating symphysis, a retromolar space, a prominent coronoid process and an asymmetrical mandibular notch. The Palomas 92 partial skeleton aligns with the Neandertals in distal humeral, proximal ulnar and femoral diaphyseal morphology, as well as infered body proportions. Although many of the isolated remains from Palomas are undiagnostic as to human group in a Late Pleistocene context, there are sufficient indicators to align these remains with the Neandertals. In no case do any of the remains exhibit uniquely derived characteristics of modern humans (*cf.,* ref. 28).

Given the concern with late Neandertal paleobiology, the considerations here are limited to the remains found *in situ* at or above the 40-43 ka cal BP levels. The comparative samples consist of MIS 5–3 western Eurasian Neandertals, MIS 5 Middle Paleolithic early modern

humans (MPMH), circum-Mediterranean Early Upper Paleolithic modern humans (EUP) (>33 ka cal BP), and western Eurasian Middle Upper Paleolithic modern humans (MUP) (≈33–24 ka cal BP).

The Mandibles Four partial mandibles were found *in situ* in the younger levels (Palomas 49, 59, 80 and 88) (Fig. 2). Palomas 59 is a left corpus lacking the full symphysis, and the others are variably complete immature specimens.

The preserved bone of Palomas 59 indicates that it had a relatively vertical symphysis but no prominent development of either a tuber symphyseos or lateral tubercles [probably mentum osseum rank 3 (29)]. The immature Palomas 49 has a similar or more retreating symphyseal profile. The dental arcade is only intact for Palomas 49, and as with other very young Neandertals (30), its bi-dc_1 external arcade diameter (35.2 mm) is beyond those of similarly aged early modern humans (Fig. 3), including that of the earlier Aurignacian La Quina-Aval 4 mandible (≈30.0 mm). Palomas 59 had a retromolar space, and Palomas 80 has a prominent coronoid process and an asymmetrical mandibular notch, but an open mandibular foramen. Most of these features align them principally with the Neandertals among MIS 5–3 humans (8).

At the same time, the mental foramina of the adult Palomas 59 (at P_4M_1) and the infant Palomas 49 and 88 (at dm_1) are moderately mesial (8,31), but the juvenile Palomas 80 mandible has an unusually mesial mental foramen, since it was distinctly mesial of the P_3P_4 break. There is little difference in lateral mandibular corpus height beween Neandertals and early modern humans (Kruskal-Wallis P = 0.251), but there is a significant (P = 0.0002) difference in breadth (SI Table 4). The other Palomas mandibles (1, 6 and 23) are with other Neandertals in corpus breadth (Fig. 4). Palomas 59, however, is among the EUP and MUP modern humans; its corpus

breadth is 2.21 standard deviations from the Neandertal mean (with the Kebara 2 high outlier trimmed, 1.97 standard deviations with Kebara 2 included).

The Dentitions The abundance of isolated teeth, plus those in Palomas 59 and 80, make several observations possible. All four of the maxillary central incisors (I^1s: Palomas 34, 73, 79 and 90) exhibit moderate to marked labial convexity, and the three lingually preserved ones have large marginal ridges and lingual tubercles (Fig. 5). The two maxillary canines (C^1s: Palomas 35 and 74) have very small lingual tubercles, and Palomas 35 has little if any shoveling (Fig. 5). Of the four P_4s (Palomas 57, 59, 78 and 87), three each exhibit a transverse crest even though only the Palomas 59 crest is pronounced (Fig. 6). All of them have a mesially displaced metaconid, and three have extra lingual cusps. Only one of the P_4s, Palomas 59, has lingual asymmetry, but it probably lacked extra lingual cusps. Yet, there are no consistent associations between these traits across the four Palomas P_4s. Of the five first and second lower molars (M_1s and M_2s: Palomas 29, 80 and 84, with one each from Palomas 59), all exhibit anterior fovea but three lack mid-trigonid crests (Fig. 7). The one M^2 (Palomas 36) has a skewed profile and centrally placed cusps.

Most of these dental occlusal traits occur in both the Neandertals and other Pleistocene (and recent) human samples, and not all Neandertals exhibit all of them (32). However, these are all traits that occur in high frequencies among the Neandertals, and Neandertals in particular have high frequencies, compared to other Pleistocene samples, of these traits occurring in combination. Of these Palomas teeth, only the I^1s and the M^2 exhibit the full suite of features increasingly considered characteristic of the Neandertals.

Root lengths, especially of anterior teeth, have been shown to largely differentiate Neandertals and Upper Paleolithic humans (33); additional data (SI Table 5) indicate a significant comparative sample difference in root lengths for all but the I^2. Of the 13 Palomas anterior teeth providing root lengths, four are below the Neandertal ranges, four are >2σ from the Neandertal means, and 77% are below the Neandertal means.

The Palomas 59 M_1 exhibits supraradicular taurodontism, and the M_2 has pronounced radicular endotaurodontism, the latter especially being characteristic of the Neandertals (34). Yet, the Palomas 29 M_2 lacks any pulp chamber expansion.

Neandertals and early modern humans have similar postcanine dental dimensions (35), but the former have greater I_1 and I_2 labiolingual crown diameters (Kruskal-Wallis $P < 10^{-6}$ for each) but contrast less in C_1 breadths (Kruskal-Wallis P = 0.025) (SI Table 6). One of the *in situ* Palomas I_1s (Palomas 21) and three of the five C_1s (Palomas 26, 54, 59) are below the Neandertal range, and the remainder of the Palomas anterior mandibular teeth are at or below the Neandertal means (two-tailed Wilcoxon P = 0.047 (I_1), 0.312 (I_2), 0.013 (C_1)).

The Postcrania In the postcrania, despite multiple elements (SI Table 1), only one disgnostic bone is stratigraphically secure in the more recent deposits, the Palomas 28 distal hand phalanx. It has a broad, rounded apical tuberosity lacking ungual spines (Fig. 8), an archaic *Homo* configuration (36,37). Neandertal distal phalangeal breadths are significantly absolutely broader than those of almost all early modern humans (Fig. 8; Kruskal-Wallis P = 0.00003) (SI Table 7), and most of them are broader relative to phalangeal length despite the relatively longer distal phalanges of the Neandertals (38). The distal breadth of the Palomas 28 phalanx (9.7 mm) falls absolutely and relatively among those archaic humans (Fig. 7, SI Table 7).

Discussion

Neandertal Affinities These considerations of the *in situ* human remains from the upper levels of the Sima de las Palomas confirm that they are best seen as late southwestern European Neandertals. There is a suite of features, including mandibular symphyseal configuration, ramal shape, dental occlusal morphology, and manual distal phalanx shape, that places them with archaic *Homo* and separate from early modern humans. Moreover, the I^1s and the P_4s, M^2, M_1s and M_2s exhibit apparently derived Neandertal occlusal traits or combinations of traits. Other retained plesiomorphous aspects lost among early modern humans or autapomorphous traits of the Neandertals (28) are not preserved or evident only on undated or older Palomas fossils. These considerations should nonetheless be sufficient to confirm that at ≈40-43 ka cal BP, in southeastern Iberia, the Middle Paleolithic population consisted of Neandertals.

Morphological Variability At the same time, it is evident that the late Palomas Neandertals exhibit a complex mix of Neandertal and more "modern" features. Three of the mandibles have mental foramina that are moderately mesial for Neandertals, but one is unusually so. Distinctive dental features such as large C^1 lingual tubercles, M_1 and M_2 mid-trigonid crest, P_4 transverse crest, lingual tubercles, mesial metaconid and lingual asymmetry, long anterior tooth roots, anterior crown dimensions, and lower molar taurodontism are reduced or variably present in the sample. None of the P_4s has all four of the "Neandertal" configurations.

It is possible to find individual Neandertal teeth or mandibles that exhibit one or more of most these "non-Neandertal" aspects, and biological variation across the Neandertals (including trends through time and clinal variation in space) has been noted (7,39-42). However, the level

of variation in these features in the Palomas late Middle Paleolithic sample is unusual for a group of Neandertals. It is possible that these contrasts with other Neandertals represent: 1) late Neandertal genetic drift in the direction of modern human morphology through isolation-by-distance in the cul-de-sac of southern Iberia, 2) an adaptive shift to local environmental constraints in some of these features, and/or 3) the product of gene flow from early modern human populations to the immediate north.

The first explanation would emphasize regional (perhaps clinal) variation among the Neandertals (*cf.*, refs.7,40). Securely dated earlier MIS 4-3 Neandertals from south of the Pyrenees [*e.g.*, Banyoles (43,44), Cova Negra (45), Gegant (46), Valdegoba (47), Zafarraya (48), plus the earlier Palomas remains] exhibit the Neandertal pattern in comparable elements (wide lateral mandibular corpori, relatively posterior mental foramina, large anterior teeth, anterior foveae and mid-trigonid crests on M_1-M_3, and asymmetrical P_4s with mesial metaconids and lingual tubercles) with minor variation in mental foramen position and a couple of the dental traits. These fossils thus imply that the Palomas variation is not merely the result of long term isolation of Iberian Neandertals through the earlier Late Pleistocene. Moreover, such isolation would not necessarily explain the presence of autapomorphous modern human traits (*e.g.*, a narrow mandibular corpus, reduced C^1 lingual tubercles, short anterior tooth roots or small anterior dental crowns) in a Neandertal population. The second explanation would imply that some of these mandibular and dental features confer an advantage on these populations, although variation in some of the features may well be selectively neutral. The third consideration would require that the earliest Aurignacian of the northern Pyrenees and elsewhere be the product of modern humans, in order to provide a geographically proximate source for gene flow. It would also invoke human biological contact across the “Ebro Frontier” during a time when there is little

evidence for cultural diffusion (10). In this scenario, the cultural contrasts across the "Ebro Frontier" would be due to behavioral choices, possibly ecologically driven, rather than isolation of the southern Iberian populations.

Conclusion

The human remains from the Sima de la Palomas in southeastern Iberia therefore document the presence of Neandertals, relatively late in the Middle Paleolithic. They help to substantiate that the Middle Paleolithic of the region was the product of Neandertals, even though diagnostic human remains associated with the very latest phases of this technocomplex in Europe remain elusive. At the same time that the Palomas humans exhibit a suite of derived Neandertal features and archaic *Homo* configurations long since lost among early modern humans, their morphological variation indicates that they deviate from the expected Neandertal ranges of variation. This pattern may be result of genetic drift in relative isolation, directional change or, perhaps more likely, populational contact to the north.

The Sima de la Palomas fieldwork has been supported by the Spanish government (CGL2005/02410/BTE; BOS/2002/02375; PB/98/0405; PB/92/0971), the Murcian government (PSH93/52; 05584/ARQ/07; CTC/DGC/SPH/063/2001; CCE/DGC/IPH/SAR0/1998; CCE/DGC/IPH/SAR/1997; CCE/DGC/IPH/SAR/011/1996; CCE/DGC/IPH/SAR/1995; CCE/DGC/IPH/SAR /1994; PSH/93/52), the municipality of Torre Pacheco, and the Earthwatch Institute (1994-2001). The landowners of Cabezo Gordo and the management of the Cabezo Gordo S.A. quarry allowed the excavations to occur. T. Rodríguez and J.L. Polo provided x-ray diffraction and fluorescence analyses. Analysis of the human remains has been funded by

CGL2007-60802/BTE (APP) and Washington University (ET). And many colleagues and volunteers over the years have enthusiastically provided assistance and expertise. To all we are grateful.

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Figure Legends

Figure 1. Schematic drawing of the current profiles of the Upper Cutting (see SI Fig. 5 and 6). A: the éboulis above northwestern corner of the excavated cutting; B: levels 2m-2o breccia containing human bones; C: projection of the éboulis scree slope, which is less perceptible in this profile than it had been in now removed sections parallel to it in the foreground; D: uppermost limit (levels ~2h-2i) of lens of burnt sediment mainly in the northeastern area of the cutting; E: lower limit of burnt ashy sediment (levels 2m-2o) in the northern and eastern area of the cutting.

Figure 2. Occlusal view of the immature Palomas (SP) 49 mandibular corpus and lateral views of the Palomas 59, 80 and 88 mandibles. Palomas 59 is in *norma lateralis*, and Palomas 80 and 88 are in the planes of their lateral corpori. Scale in centimeters.

Figure 3. Bivariate plot of external bi-deciduous canine (dc_1) dental arcade breadth versus developmental age for immature Late Pleistocene human mandibles. Symbols: black diamond: Palomas 49; gray circles: Neandertals; black squares: MPMH; black triangle: EUP modern human (La Quina-Aval 4); open triangles: MUP modern humans. Ages are based on dental calcification relative to extant humans.

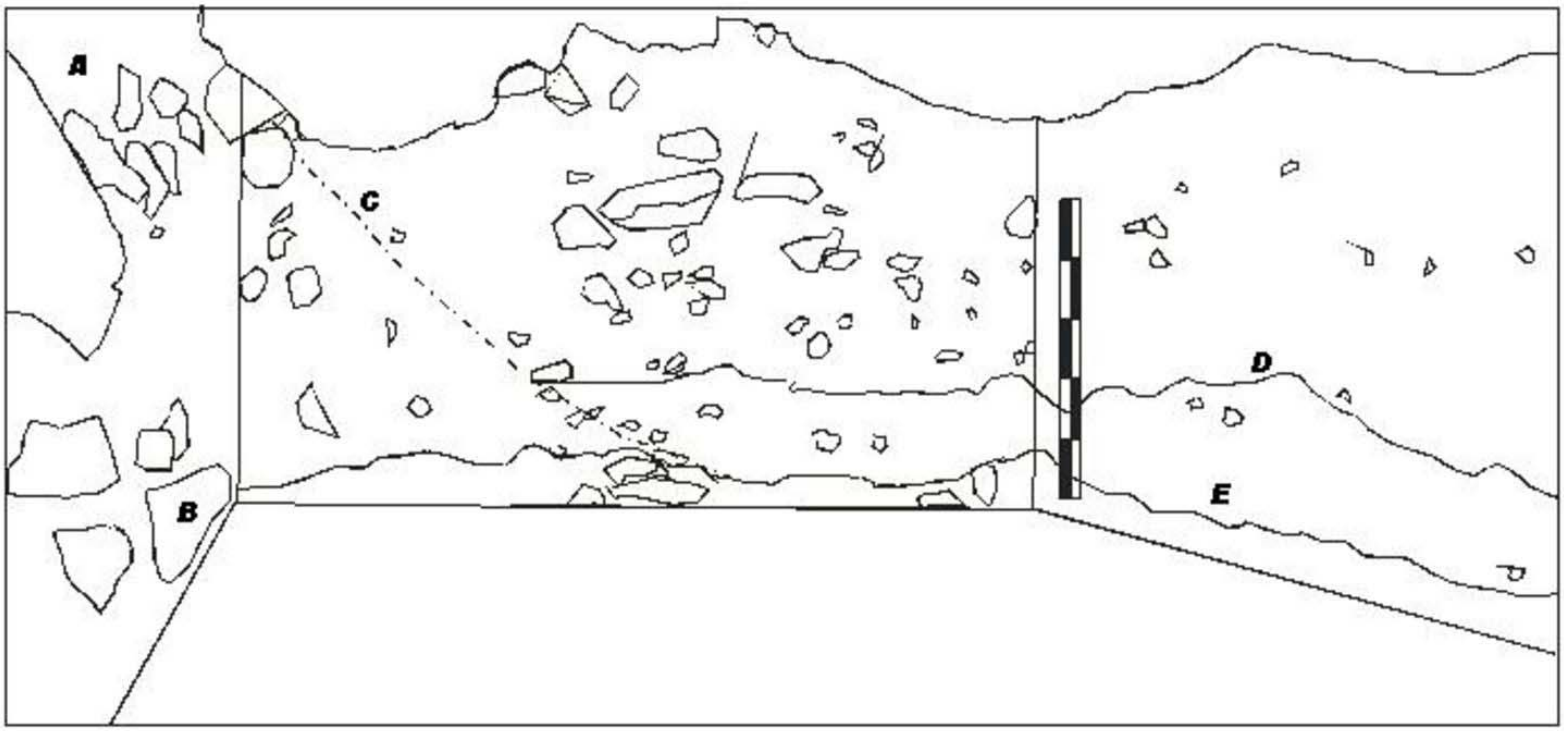
Figure 4. Bivariate plot of mandibular corpus breadth versus height at the mental foramen, for Late Pleistocene mature mandibles. Symbols as in Fig. 2; numbered symbols are for Palomas 1, 6, 23 and 59, the first three of which are geologically older than Palomas 59 or undated. The early modern humans with high corpus breadths are Qafzeh 9 and Skhul 4 (MPMH), Nazlet Khater 2 (EUP) and Cro-Magnon 1 (MUP); the high Neandertal outlier is Kebara 2.

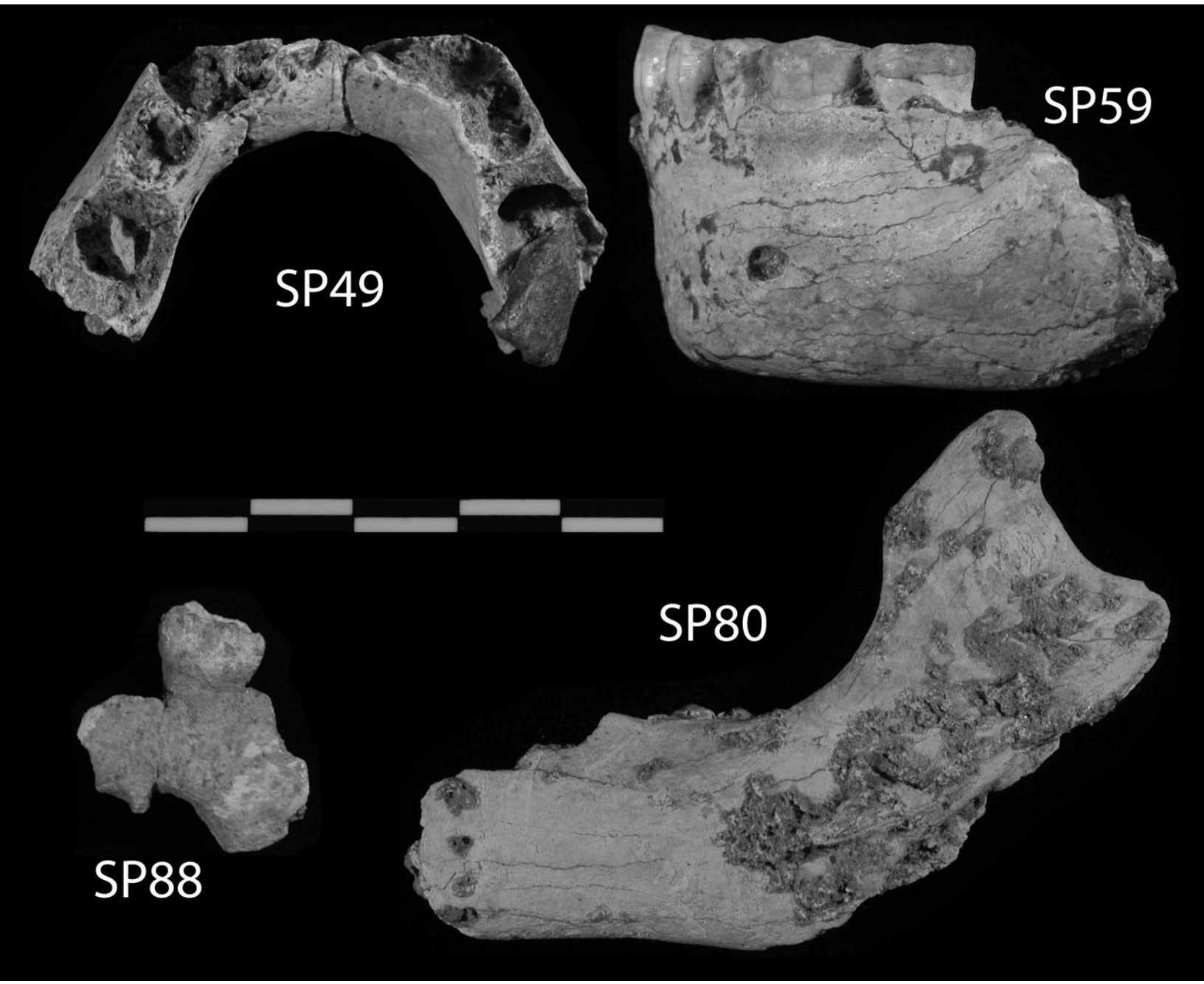
Figure 5. Lingual views of Palomas (SP) maxillary central incisors (I^1s) (SP 34, 79 and 90) and maxillary canines (C^1s) (SP 35 and 74). Scale in millimeters.

Figure 6. Occlusal views of Palomas (SP) mandibular second premolars (P_4s). Scale in millimeters.

Figure 7. Occlusal views of Palomas (SP) molars. SP 36: maxillary M^2. SP 59: mandibular M_1 and M_2. SP 80: mandibular M_2. SP 29: mandibular M_2; SP 84: mandibular M_1. Scale in millimeters.

Figure 8. Bivariate plot of distal phalangeal breadth versus articular length for Palomas 28 and Late Pleistocene samples. Symbols as in Fig. 2. Given uncertainties in digit assignment for isolated ray 2-4 distal phalanges, values are averaged for those individual preserving multiple distal phalanges to provide an individual value.


A
B
C
D
E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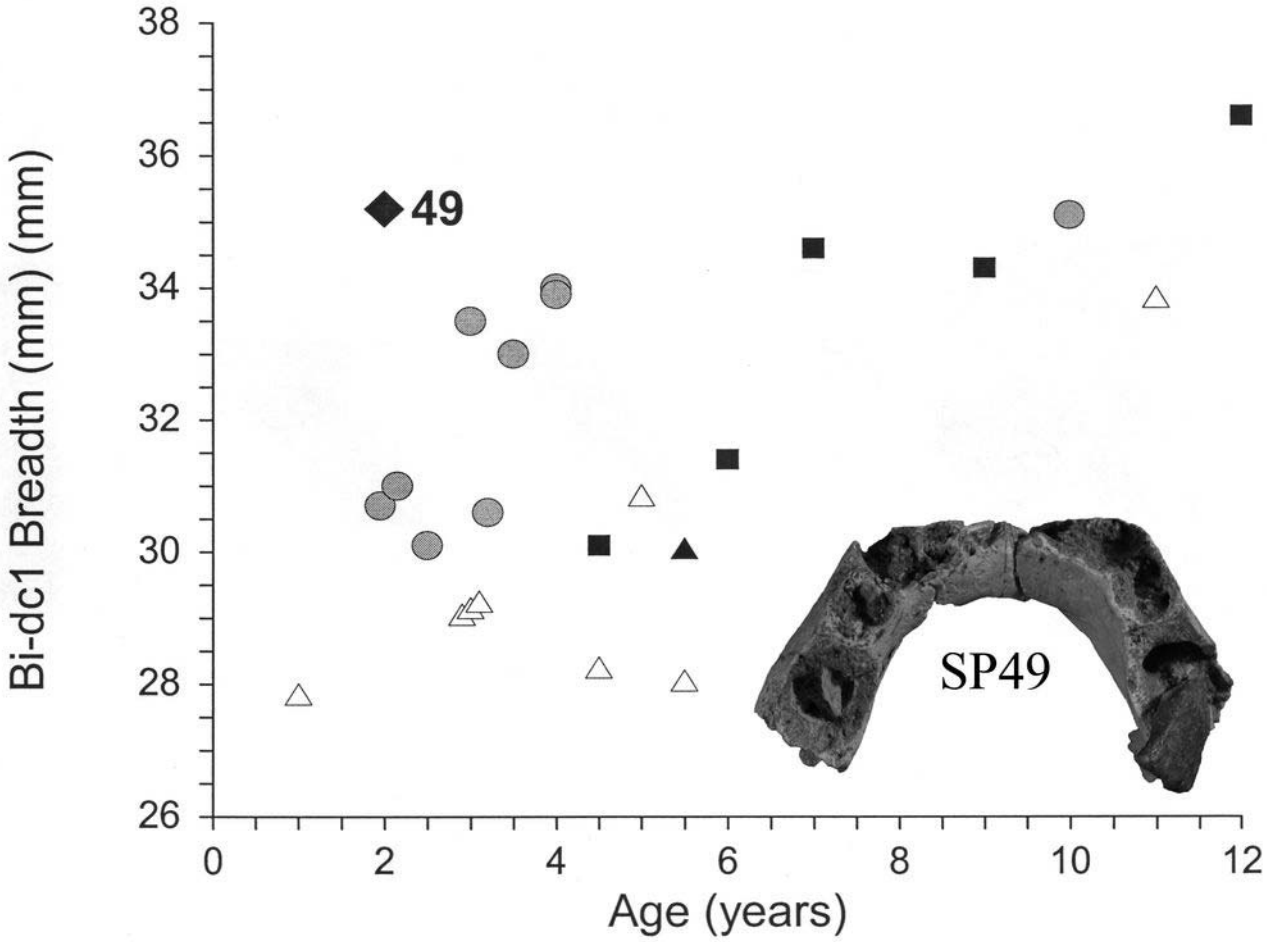
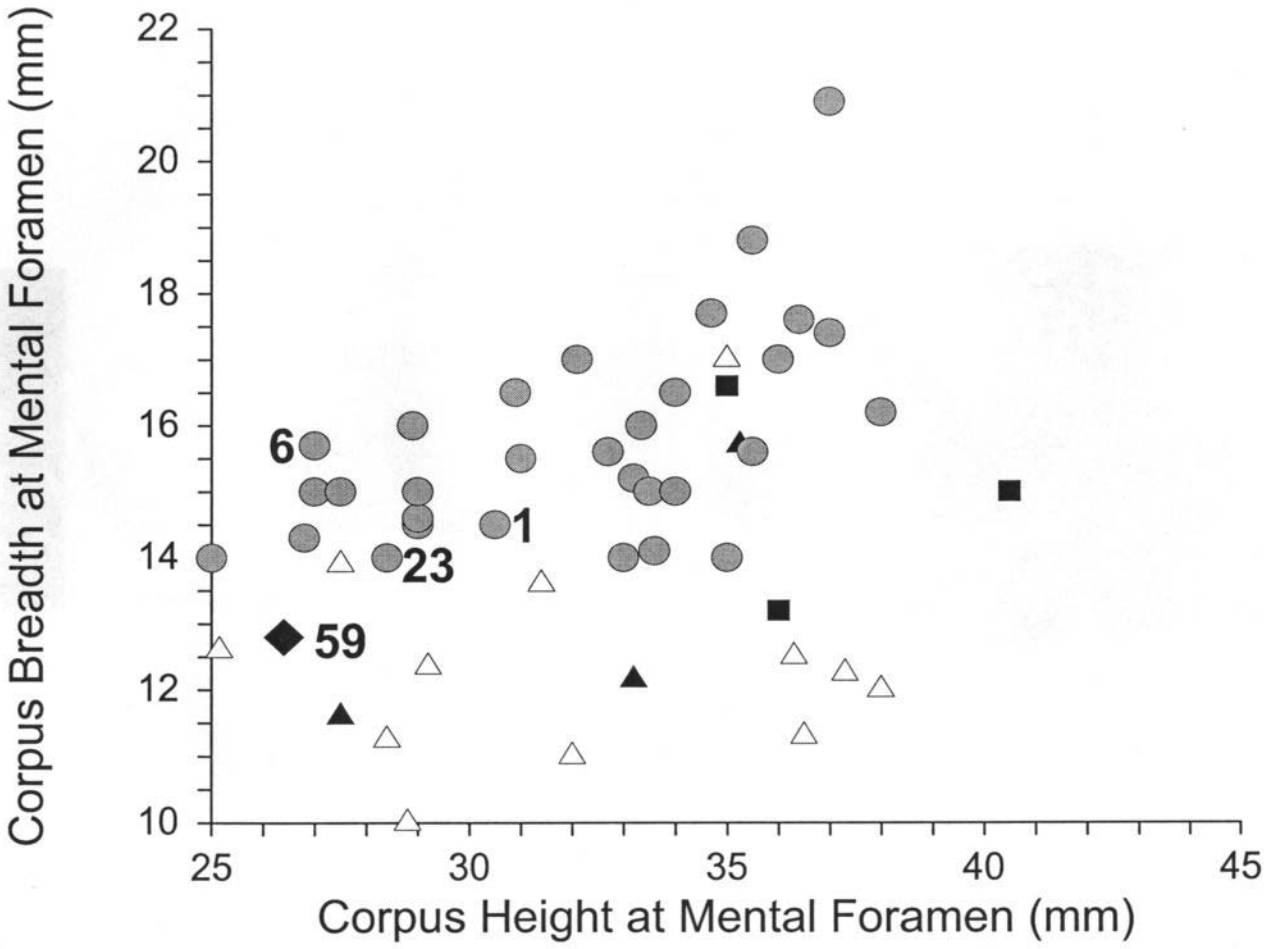
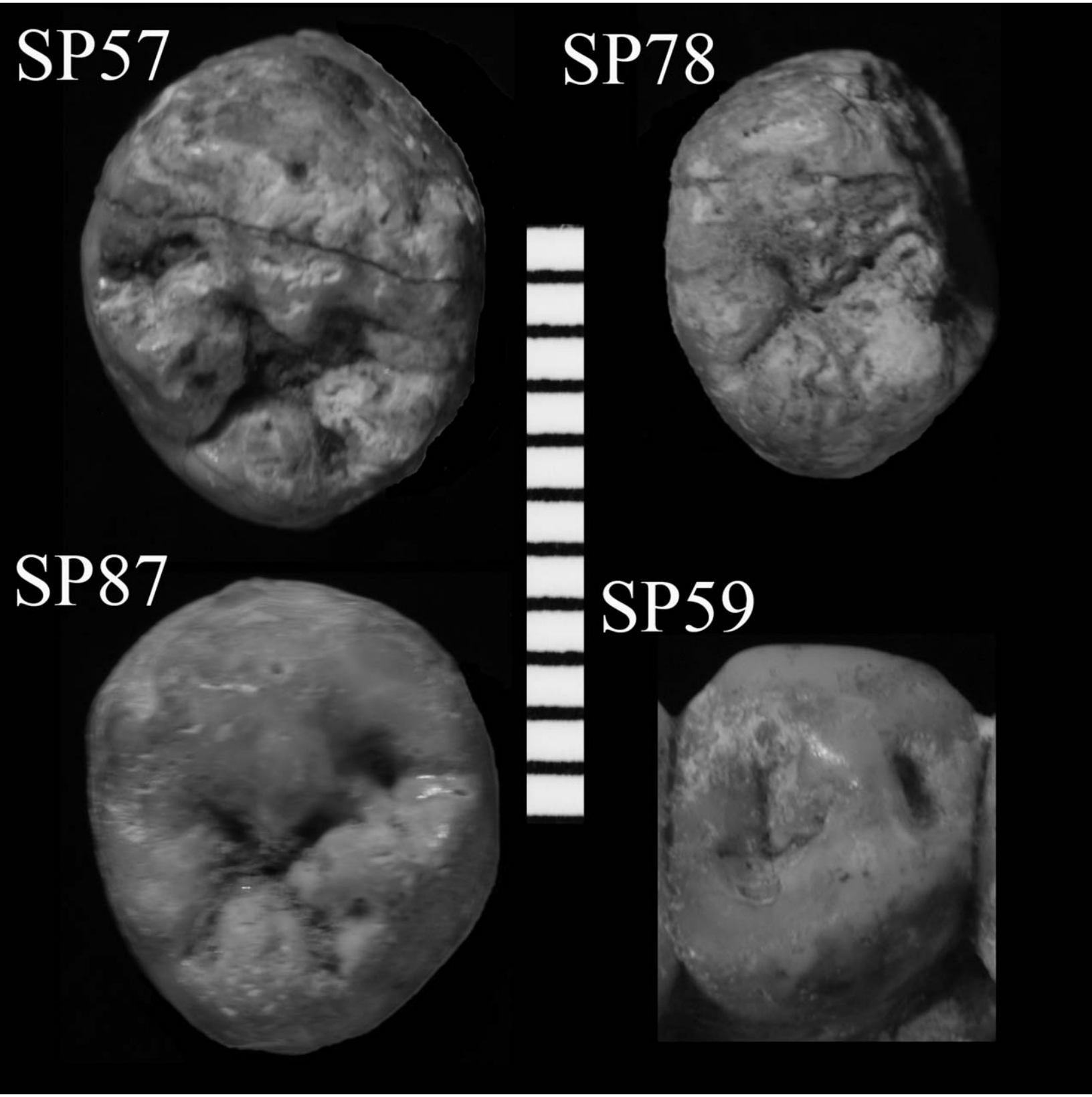
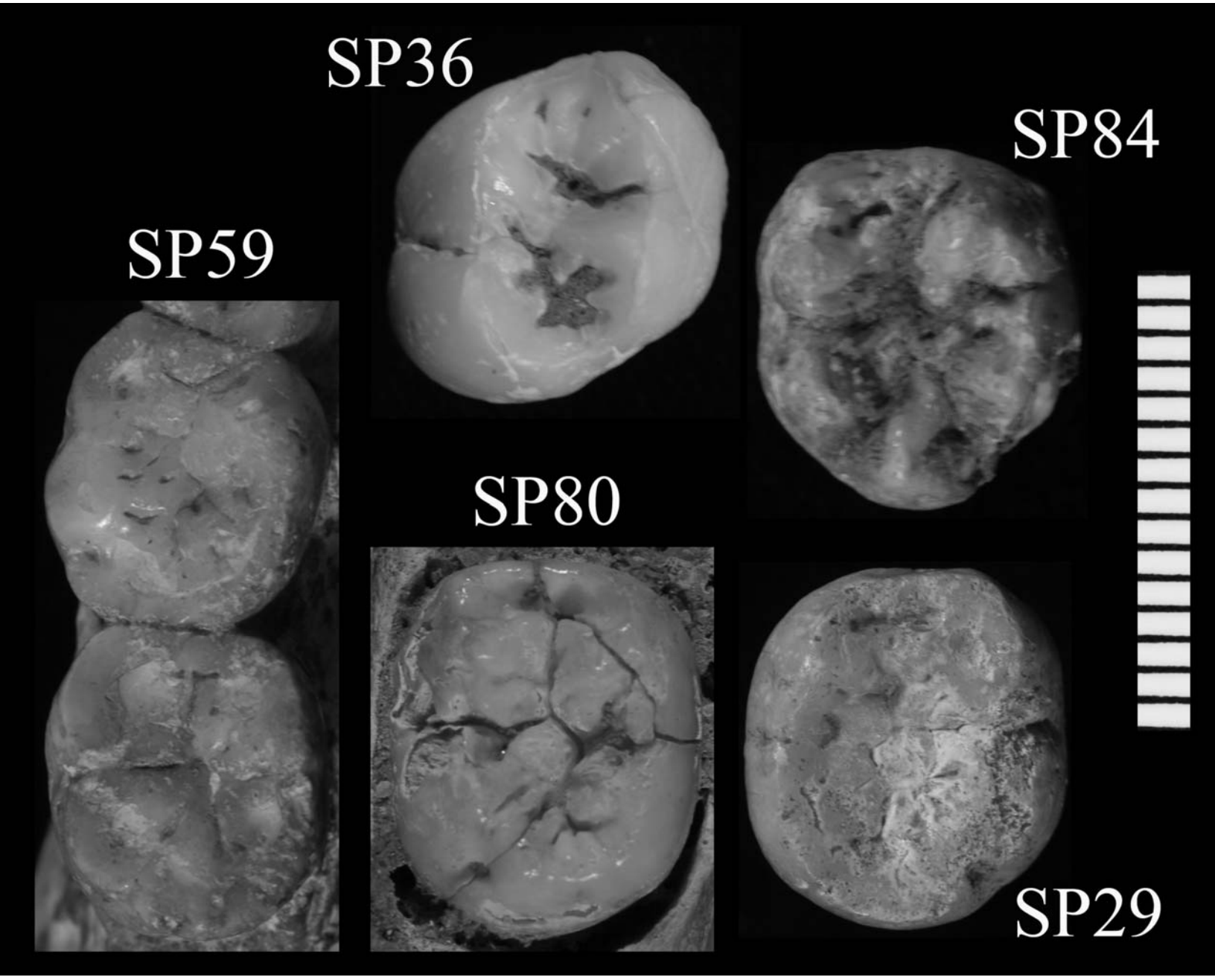
SP59
SP80
SP88

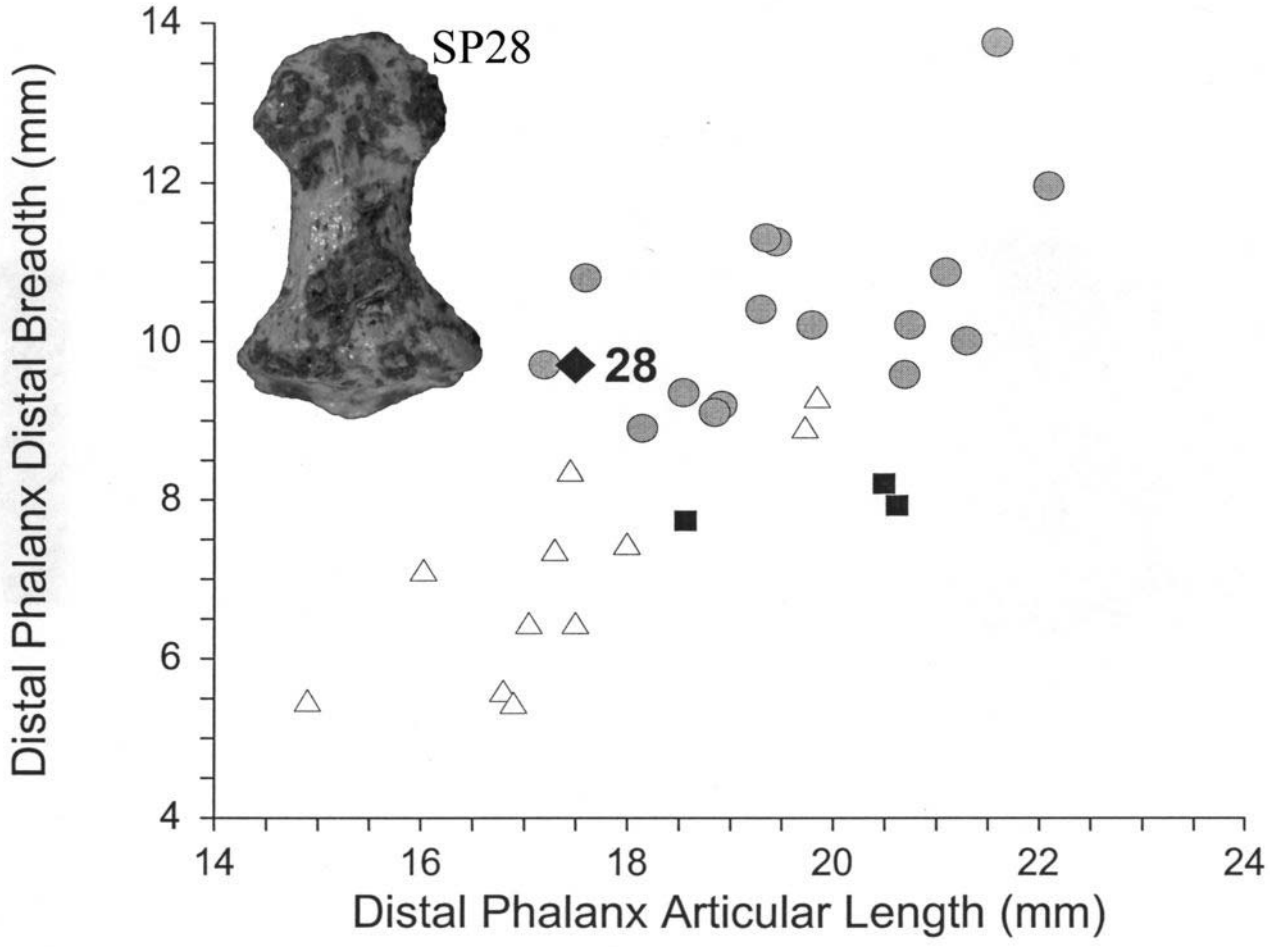

Bi-dc1 Breadth (mm) (mm)
38
36
34
32
30
28
26
0
2
4
6
8
10
12
Age (years)
49
SP49


Corpus Breadth at Mental Foramen (mm)
22
20
18
16
14
12
10
25
30
35
40
45
Corpus Height at Mental Foramen (mm)
6
1
23
59

SP34
SP79
SP90
SP35
SP74


SP57
SP78
SP87
SP59


SP36
SP84
SP59
SP80
SP29


SP28
28
Distal Phalanx Distal Breadth (mm)
Distal Phalanx Articular Length (mm)
14
12
10
8
6
4
14
16
18
20
22
24