

Neandertal Mandibles from the Sima de las Palomas del Cabezo Gordo, Murcia, Southeastern Spain

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KEY WORDS Late Pleistocene; Europe; symphysis; mental foramen; mandibular notch

ABSTRACT The Middle Paleolithic levels of the Sima de las Palomas have yielded eight partial mandibles (Palomas 1, 6, 7, 23, 49, 59, 80, and 88). Palomas 7, 49, 80, and 88 are immature, and Palomas 49, 59, 80, and 88 are among the latest Neandertals (~40,000 cal BP). Palomas 1 is geologically older (~50,000–60,000 cal BP), and the other three were found ex situ. The mandibles exhibit a suite of characteristics that align them with the Neandertals among later Pleistocene humans, including symphyseal morphology, symphyseal orientation, corpus robusticity, distal mental foramen position, retromolar space presence, wide immature dental

arcade, and high-coronoid process with an asymmetrical mandibular notch. However, Palomas 6 lacks a retromolar space, Palomas 59 has a narrow lateral corpus, and Palomas 80 has a mesial mental foramen and open mandibular foramen. The Palomas mandibles therefore help to document that the late Middle Paleolithic of southern Iberia was the product of Neandertals. They also reinforce the presence of variability in both metric and discrete aspects of Neandertal mandibular morphology, both within and across samples, some of which may be temporal and/or geographic in nature. *Am J Phys Anthropol* 000:000–000, 2010. © 2009 Wiley-Liss, Inc.

Western Eurasian Neandertal mandibles have been shown to exhibit a constellation of features, which distinguish them morphologically from the mandibles of both earlier *Homo* mandibles and early modern humans (Kallay, 1970; Quam and Smith, 1998; Stefan and Trinkaus, 1998a; Rosas, 2001; Lebel and Trinkaus, 2002; Richards et al., 2003; Soficaru et al., 2006). These features include aspects of overall metric proportions as well as a series of discrete traits that either indirectly reflect those proportions or appear independent of them. This constellation of features nonetheless exhibits variation within site-specific samples and across the Neandertal range in time and space (Smith, 1976; Wolpoff et al., 1981; Trinkaus, 1983; Stefan and Trinkaus, 1998b; Rosas et al., 2006). In this context, we present here eight Neandertal partial mandibles from the Sima de las Palomas, southeastern Spain. Although three of them were found out of context, and therefore may derive from different stratigraphic horizons than those found in situ, these mandibles may serve to further augment the range of variation in Neandertal mandibular morphology.

THE PALOMAS MANDIBLE SAMPLE

The mandibles

The Palomas Neandertal sample contains eight partial mandibles, four of which are mature (Figs. 1–3) [for complete notes on preservation and ages-at-death of the mandibles, see Supporting Information I]. As such, the Palomas mandible sample is the largest Late Pleistocene Neandertal one known; it is exceeded in size among Neandertal lineage samples only by the Middle Pleistocene ones from Krapina and Atapuerca-SH (Radović et al., 1988; Rosas, 1995).

Palomas 1 retains most of the mandible from near the symphysis to middle of the ramus on one side, but it was heavily damaged in breccia in situ. The right corpus and anterior ramus are more intact than the left side, but left corpus provides a reliable corpus height. Based on dental wear, it represents an older but not geriatric individual. Palomas 6, 23, and 59 consist of mature corpora, the first two extending from the symphysis to the distal M_3 or inferior ramus on the left and right sides, respectively, and the third including the left I_2 to M_3 corpus. Palomas 23 and 59 have modestly worn dentitions and represent young adults; Palomas 6 was mature, but the absence of tooth crowns prevents further aging. The 1.5–2.5-year-old Palomas 49 mandible retains most of

Additional Supporting Information may be found in the online version of this article.

Grant sponsor: Torre Pacheco and the Earthwatch Institute (1994–2001); Grant sponsor: Spanish Government; Grant numbers: CGL2005/02410/BTE, BOS/2002/02375, PB/98/0405, and PB/92/0971; Grant sponsor: Murcian Regional Government; Grant numbers: PSH93/52, 05584/ARQ/07, CTC/DGC/SPH/063/2001, CCE/DGC/IPH/SAR0/1998, CCE/DGC/IPH/SAR/1997, CE/DGC/IPH/SAR/011/1996, CCE/DGC/IPH/SAR/1995, CCE/DGC/IPH/SAR/1994, PSH/93/52.

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Received 21 May 2009; accepted 25 September 2009

DOI 10.1002/ajpa.21223

Published online in Wiley InterScience
(www.interscience.wiley.com).



Fig. 1. Lateral views of the Palomas 1, 6, 23, and 59 mandibular corpora and ramus. The mandibles are in the plane of the lateral corpus, not in *norma lateralis*. Scale in centimeters.

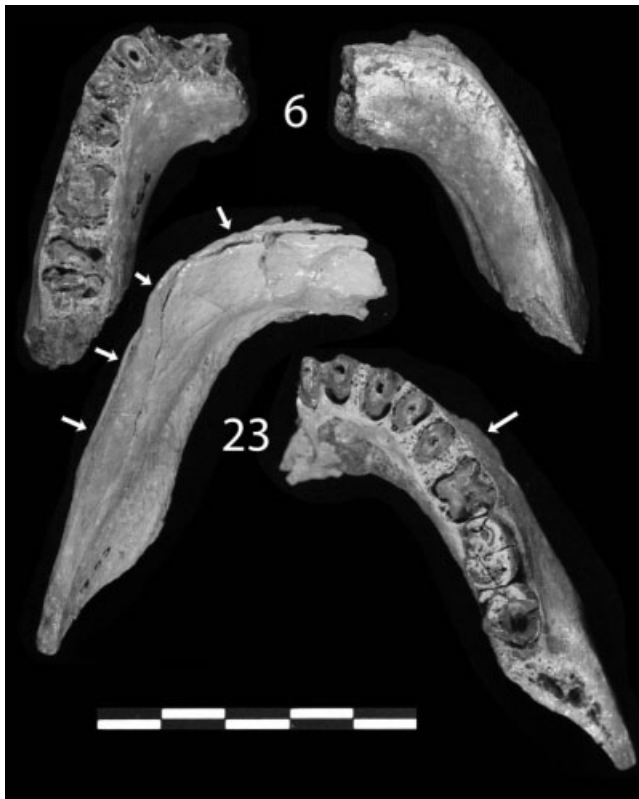


Fig. 2. Superior and inferior views of the Palomas 6 (above) and 23 (below) mandibles. The orientations of the Palomas 6 and 23 mandibles are based on the assessments of their symphyseal midlines. All the crowns of the Palomas 6 teeth and all but portions of the molar crowns of Palomas 23 were lost through burning in situ. The anterolateral margin of the inferior corpus of Palomas 6 was eroded, such that the rugosity reflects chipping and abrasion and not a morphological feature. The basilar flange on the Palomas 23 mandible is indicated by several arrows. Scale in centimeters.

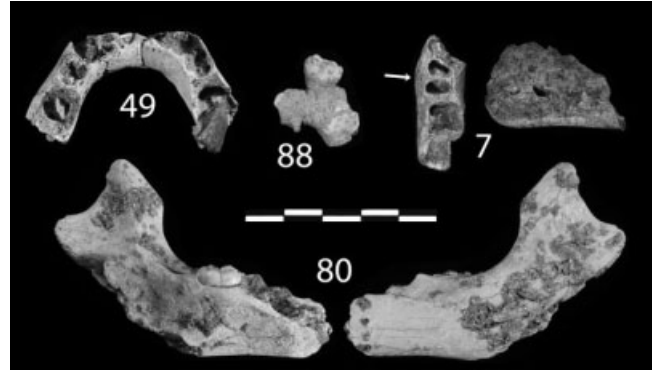


Fig. 3. Occlusal views of the Palomas 7 and 49 mandibles, lateral views of the Palomas 7, 80, and 88 mandibles, and medial view of the Palomas 80 mandible. The incipient basilar flange on the Palomas 7 mandible is indicated by the arrow. Scale in centimeters.

the corpus, from the right dm_2 crypt to the left dm_2/M_1 interdental septum. Palomas 7 is a left corpus section, from the distal dc_1 socket to the mesial side of the M_1 crypt, of a 3.5–4.5-year-old child. Palomas 80 is a left corpus and ramus piece of an 11–12-year-old early adolescent, from the lower portion of the P_3/P_4 interdental septum to the middle of the ramus through the mandibular foramen. Palomas 88 is a lateral corpus fragment between the dm_2 and the mental foramen of a 2–3-year-old infant.

The Palomas 6 and 23 mandibles were heated in situ, which resulted in the loss of most (Palomas 23) or all (Palomas 6) of the tooth crowns and discoloration, but the heating does not appear to have affected their basic proportions or surfaces. Palomas 6 did experience surface bone loss along the external margin of the inferior corpus, and an unusual external flange of bone on the inferior corpus of Palomas 23 became partially separated. The only pathological abnormalities evident on the Palomas mandibles involve anomalies of the Palomas 59 M_2 ; the mandibular corpus was not affected externally by these changes.

The context of the Palomas mandibles

The Sima de las Palomas, Cabezo Gordo, Torre Pacheco, Murcia, Spain (37° 47' 59" N, 0° 53' 45" W) consists of a Late Pleistocene in-filling of a ~18-m vertical shaft formed into dolomitic limestone, which was largely emptied during the 19th century by miners (Fig. S9; Walker, 2001; Walker et al., 2008). The remaining stratigraphy, which consists primarily of a column of sediment along one side of the miners' shaft, has been excavated in its lowest portion (the Lower Cutting), in a small portion ~5 m above the bottom of the sediment column (the Intermediate Cutting), and in the uppermost 3–4 m (the Upper Cutting). The Upper Cutting (Fig. S10) consists of a largely brecciated scree, or éboulis (Conglomerate A), sloping down from the west side, overlain to the east by an infilling of softer, gritting sediment containing angular stone clasts. The two sediment components are separated by a dark-gray burnt horizon, the Upper Burnt Layer.

The brecciated scree, or éboulis, of Conglomerate A lies on an extensive burnt horizon (the Lower Burnt Layer). This Lower Burnt Layer covers, in turn,

another bone-bearing breccia, which is heavily cemented (Conglomerate B), which in turn covers a much looser scree or éboulis. Most of these levels in the Upper Cutting contain abundant lithic and faunal remains and variously complete human fossils.

Four of the human mandibles (Palomas 49, 59, 80, and 88) were found between 1996 and 2004 in situ during excavation in Levels 1A, 2f, 2d, and 2g, respectively, of the softer sediment in-filling of the Upper Cutting, above the Upper Burnt Layer. The Palomas 1 mandible (and maxillary dentition) was removed in 1991 from the exposed brecciated level slightly below the Upper Burnt Layer, or in Conglomerate A. The remaining three mandibles, Palomas 6, 7, and 23 were found in 1993 and 1995 ex situ among the mine rubble on the adjacent hillside, along with a substantial portion (27%, $N = 97$) of the Palomas human remains (cf., Walker et al., 2008: Supporting Information Table 1). Those remains therefore derive from the site, but their stratigraphic positions are unknown. It is plausible, given the similarity of the burning on Palomas 6 and 23 to bones in the Lower Burnt Layer that they derive from that portion of the Upper Cutting.

A combination of accelerator mass spectrometry radiocarbon, laser ablation multicollector plasma mass spectrometry uranium-series, optically stimulated luminescence, and paleoclimatic correlation dating places the remains from above the Upper Burnt Layer in the Upper Cutting to ~40,000 cal years BP (~35,000 ^{14}C years BP) and those in Conglomerate A to ~50,000–60,000 cal years BP (cf., Walker et al., 2008 for dating details). The deeper levels of the sediment column should extend back through much of the Late Pleistocene. Only Middle Paleolithic lithic remains have been found in situ and in the material disturbed by the 19th century miners.

The geological age of Palomas 49, 59, 80, and 88 makes them among the youngest of the known Neanderthal remains. They are approached in age in Iberia only by the moderately older Oliveira and El Sidrón Neanderthal samples (Rosas et al., 2006; Trinkaus et al., 2007), although there are younger Middle Paleolithic sites in Iberia south of the Ebro Valley (Zilhão, 2006). It also places them approximately contemporaneous with early modern humans in southeastern Europe (Trinkaus et al., 2003) and just to the north of the Pyrenees if the earliest Aurignacian there was the product of modern humans (Zilhão, 2006).

The Palomas 1 mandible is moderately older, similar in age to many European Neanderthals. The geological ages of the last three Palomas mandible are not known; if they derive from the Lower Burnt Layer, they are likely to be only moderately older in the Late Pleistocene than Palomas 1. They are assessed here as though they are approximately contemporaneous with the more securely dated remains.

MORPHOLOGY OF THE PALOMAS MANDIBLES

The Palomas 1 mandible

The distorted nature of the Palomas 1 mandible only permits some corpus height and breadth measurements, combining both sides, as well as observations of several discrete traits. As preserved and through the visual reconstruction of the right corpus and ramus using observations from the left corpus (Figs. 1 and S1), an overall impression of its proportions can be obtained. The associated maxillary fragments provide little morphological information.

The symphysis is sufficiently intact and undistorted to the I_1/I_2 interdental septum to indicate an anterior buccal depression below the right I_1 to the I_2/C_1 , up to 16.7 mm from the alveolar margin. The symphysis is largely vertical or slightly retreating relative to the alveolar plane, although damage makes any such assessment tenuous; it was not markedly retreating. It exhibits a gentle swelling, but the mental trigone area is not preserved. It is conservatively scored as mentum osseum rank 2–3 [retreating (2) or vertical (3), with a clear but nonprojecting mental trigone (cf., Dobson and Trinkaus, 2002)] (Tables 1 and S2).

The right mental foramen is single, opens laterally and slightly posteroinferiorly, and it is located slightly below the vertical middle of the corpus. The left one is indicated by its posterior margin. The right one is below the P_4 , and the left one is below the P_4/M_1 interdental septum, assuming that the foramen is round and single. The lateral eminence begins below the M_2 , but it is not prominent. The gonial angle is evenly rounded, and there is a smooth and rounded concavity in lateral view between its anterior extent and the basilar margin of the corpus.

There is a distinct retromolar space on the left side, ~10 mm from the distal M_3 to the anterior ramus as preserved. Visual placement of the right anterior ramus to an anatomically correct position (see Fig. 1) provides a similar retromolar space. The right coronoid process is high and prominent, with a marked endocoronoid buttress. The inferior two-thirds of its anterior margin are concave, and the superior portion (damaged) would have been anteriorly projecting relative to the lower portion. The shape of the mandibular notch cannot be directly assessed. However, the coronoid process is high; the current posterior height (basilar margin to coronoid tip) is 73.5 mm, and photographic reconstruction places it ~80 mm above the inferior corpus margin. It would require an exceptionally high condyle to make the resultant notch evenly rounded, and so it was probably asymmetrical with a high-coronoid process.

The Palomas 6 mandible

Palomas 6 retains the left symphysis and lateral corpus (Figs. 1, 2, 4, and S3). The anterior symphyseal surface retreats relative to the alveolar plane (the symphysis is insufficiently complete at midline to measure its anterior angle), but one can see the lateral extent of the mental trigone below the distal I_1 and the I_2 alveoli. The trigone is ~5 mm high at the break slightly lateral of the midline, and it ends laterally below the I_2/C_1 interdental septum. In combination with the symphyseal retreat, this provides a mentum osseum rank of two. It is not possible to determine how straight the midline profile was given damage. There is an anterior buccal depression below the I_2/C_1 , 11.5-mm high and 7.2-mm wide, but damage precludes determining if it extended below the I_1 .

The anterior dental arcade appears to angle strongly around the C_1 , with a more transverse incisal profile. However, this impression may be exaggerated by the loss of the incisors and their associated alveolar bone, especially labially. The lingual symphysis has a modest planum alveolare, which descends smoothly to a thickening of the symphysis. The thickening produces an even convexity from the planum alveolare to the basilar mar-

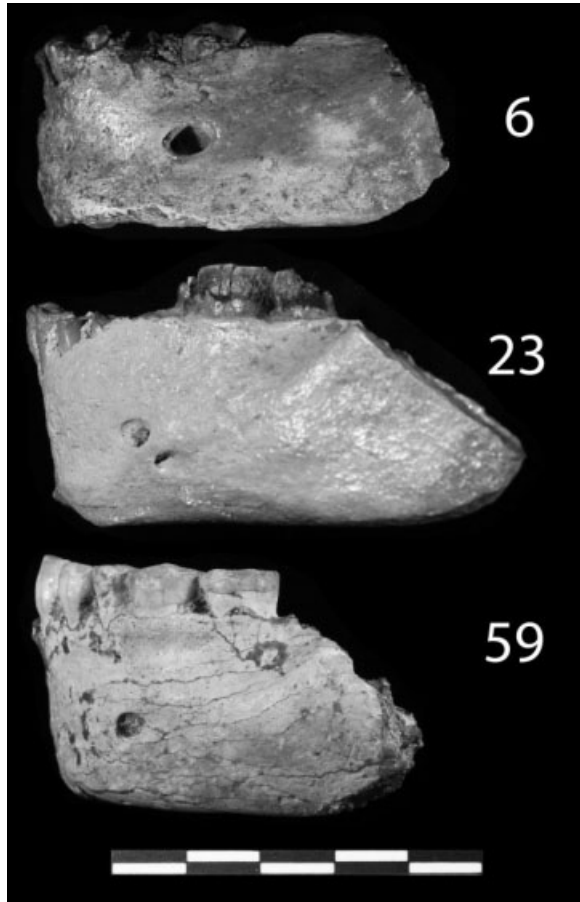


Fig. 4. The Palomas 6, 23, and 59 mandible corpora in approximate *norma lateralis*. Palomas 23 preserves the full midline, and Palomas 6 preserves the inferior midline, but Palomas 59 is complete mesially only to the I_2 alveolus. The inferiorly projecting bone on Palomas 23 is a partially detached portion of the extra flange of bone. Scale in centimeters.

gin, and so it is hard to describe it as either superior or inferior transverse torus, rather than just a transverse torus. The effect is a thick symphysis, which spans the height of the bone. There are two small genioglossal tubercles, projecting less than 1 mm.

The region of the digastric impressions has been altered through erosion into a rugose margin along the anterior and lateral portions of the inferior corpus, as opposed to the usual tear-dropped insertion areas for the anterior belly of the muscle. Along the anterior and lateral margins of the eroded inferior surface, from below the C_1 to the P_4 , there is a small anterolateroinferior eversion of the external corpus. This remaining lip of bone is unusual, both among Neandertals and recent humans, because the associated corpus margin is usually rounded from lateral to inferior with a variably present anterior marginal tubercle (Rosas, 2001). Moreover, the projecting lip may have been larger, prior to the post-mortem erosion that removed the digastric impressions. It resembles the similar lip of bone on Palomas 23 (see below), but there is no evidence of a fusion line such as is present on Palomas 23.

The lateral corpus retains the thickness present in the symphysis, with its corpus breadths exceeding those of

Palomas 1 despite a shorter corporeal height (Table S3). Its external surface has a prominent lateral eminence below the M_2 , which appears more as a rounded tubercle ~12-mm anteroposterior and ~5-mm high, than as the usual swelling for the eminence. The posterior end of this swelling is separated by a slight depression from the anteroinferior end of the ramal margin.

Below the P_4/M_1 interdental septum, but extending below both the P_4 and the mesial M_1 root, is a very large mental foramen. Its midpoint is midway between the alveolar and the basilar margins. It is ellipsoid in shape, opens directly laterally, and has the orientation of its maximum dimension sloping slightly anteroinferior to posterosuperior. Radiographically (Fig. S3), it is associated with a large inferior alveolar nerve canal, larger in vertical dimension than the foramen, suggesting that the mental foramen dimension is likely to be an anatomical variant and not the result of the burning. Medially, there is an angle along the mylohyoid line, with a posteriorly widening concavity below it. The inferomedial surface is smooth.

It is not possible to determine directly whether the mandible had a retromolar space. However, if the line of the anterior ramal margin, as preserved below the distal M_2 and the mesial M_3 , is extended in an even arc posterosuperiorly, and the original M_3 crown is given a conservative mesiodistal diameter of ~10 mm (Late Pleistocene pooled sample: 11.6 ± 0.8 mm, $N = 66$), the line of the anterior ramal margin would cross the distal portion of that M_3 crown in *norma lateralis*. Palomas 6 therefore almost certainly lacked a retromolar space.

The Palomas 7 immature mandible

The lateral corpus appears to have some angulation around the dc_1/dm_1 interdental septum, but the anterior breakage prevents determining how pronounced was the angle (Figs. 3 and S4). Inferiorly, this is accentuated by a rounded flange of bone on the external basilar margin.

The flange begins mesially below the dc_1 , is most prominent below the mesial dm_1 , and then gradually fades away by the mesial M_1 crypt. It is part of a continuous rounding with the inferior margin of the corpus, with no evidence of a digastric insertion or rugosity. There is a shallow sulcus along the superior margin of the flange, which separates it from the lateral surface of the corpus. The flange resembles what could be the juvenile manifestation of the external inferior flanges of Palomas 6 and 23 (see Fig. 3).

There are two mental foramina, a slightly larger one below the dm_1/dm_2 , which opens posteriorly, and a smaller one below the mesial dm_1 root, which opens anteriorly.

The Palomas 23 mandible

The symphysis of Palomas 23 (Figs. 1, 2, 4, and S5) retreats (anterior symphyseal angle: infradentale-pogonion relative to the alveolar plane: 76°), but it is vertically straight in *norma lateralis* right. There is a hint of a mental trigone, and therefore it has a mentum osseum rank of two. Lingually, there is a prominent superior transverse symphyseal torus but no inferior transverse torus. There does not appear to be a planum alveolare, although one might construe the superior portion of the superior transverse torus to constitute a planum alveo-

lare. There are no anterior buccal depressions. The genio-glossal tubercles are small, rounded, and nonprojecting.

The digastric fossae are delineated anteriorly, medially, posteriorly on their medial halves, and, to some extent, posterolaterally. There is an externally (anteriorly and laterally) directed lip of bone across the anterior and lateral inferior margins of the corpus, from just left of the symphyseal midline to the M_3 . Especially below the canine and the premolars, the extra bone forms a laterally extending crest of bone, which is most prominent below the P_4 . It is extra bone laid down and partially fused onto the external inferior corpus margin. The lip of bone has become partly separated from the corpus across the symphysis and distally to the P_4/M_1 due to the burning of the mandible, and a fusion line with the normal, rounded inferior corpus margin is apparent to its posterolateral end below the M_3 , just anterior of the inferior gonial flare. Anteriorly, the extra lip of bone forms the external margin of the otherwise normal digastric impressions, but laterally it is distinct from that muscle insertion. It does not appear to have altered the remainder of the mandibular corpus morphology.

The lateral corpus has parallel alveolar and basilar margins. It is minimally taller than Palomas 6 and a few millimeters shorter than Palomas 1. The mental foramen is double, with the larger foramen positioned more anterosuperiorly and opening in that direction, and the smaller one positioned and opening posteroinferiorly. The larger foramen is under the M_1 , and the smaller one is below the M_1/M_2 interdental septum. The lateral eminence is below the M_3 and is small. Its position is indicated mostly by the beginning of the anterior ramal root. Internally, the mylohyoid line is weak with little angulation. It is also well below the alveolar plane at the M_3 .

The anterior ramal root is ~3 mm posterior of the M_3 at the alveolar plane, and there is the beginning of a retromolar alveolar surface preserved distal of the M_3 . The two features combine to indicate the presence of at least a small retromolar space.

Only a portion of the gonial angle is preserved; it is evenly rounded, continuing the line of the basilar margin. If one visually deletes the extra lip of bone back to the region of the M_3 along the join between it and the corpus, the Palomas 23 mandible would have had a modest concavity in the inferior margin just anterior of the rounding for the gonial angle.

Only the inferior portion of the medial pterygoid insertion is preserved, but it is remarkable for the absence of rugosity or tubercles. This does not indicate whether a prominent superior medial tubercle was present.

Palomas 49 immature mandible

The anterior symphysis is damaged superiorly, and it is best considered slightly retreating to vertical, depending upon how broad one makes the deciduous incisors and hence the estimated position of infradentale (Figs. 3 and S6). Given bone loss and crushing in the region of the anterior symphysis, it is not possible to determine whether a trigone was present.

The lingual symphysis presents a clear planum alveolare, although it may be due to the forming permanent incisor crowns, which should have reached at least half of their crown formation by the age-at-death of Palomas 49 (Smith, 1991). There is no evidence of a transverse

torus. The digastric fossae are present on the inferior surface of the symphysis, with distinct concavities but no rugosity, plus a prominent midline peak. The better preserved right one is 2.8-mm anteroposterior and 4.9-mm longitudinally (anteromedially to posterolaterally).

The mental foramina are single on both sides, and each one is below the middle of the dm_1 . The right one is slightly smaller than the left one.

On both sides of the corpus, there appears to be a gentle swelling of bone along the inferolateral margin. It is continuous on the right side and ends posteriorly in a small tubercle; the postmortem separation of it from the more superior lateral corpus makes it unclear whether it is a fossilization artifact or reflects the original morphology. It is evident for ~5 mm below the mental foramen on the left side, with a slight sulcus above it. Its location and form suggest a developmental precursor to the flanges of Palomas 6, 7, and 23, but the damage to the right side and the minimal development on the left side makes such an interpretation tenuous.

The Palomas 59 mandible

The Palomas 59 (Figs. 1, 4, and S7) symphyseal morphology assessment is approximate given damage to the region. However, the anterior midline appears to have been relatively vertical with a modest retreat. There is no evidence of the trigone on the preserved portion below the I_2 , but it is likely to have been mentum osseum rank 3, vertical without projection of the trigone; it is conservatively scored as 2-3 (Tables 1 and S4). Lingually, there is no planum alveolare. There is lingual inferior swelling more laterally, so that there may have been a small inferior transverse torus.

The single mental foramen has its middle at the mesial edge of the mesial M_1 root. It is therefore best considered as intermediate between " M_1 " and " P_4/M_1 " designations. The corpus has parallel alveolar and basilar planes with a pronounced basilar margin. There is no evidence of an inferolateral eversion similar to those on Palomas 6 and 23. The modest lateral eminence is below M_2 and M_3 . The mylohyoid line is rounded, and it was well below the M_3 alveolar margin. The mylohyoid line to alveolus distance cannot be accurately measured at the M_3 , because both ends must be estimated; continuing the lines of the mylohyoid line and the alveolar plane provides a height of ~6 mm. The region of the retromolar space is not preserved, but one can estimate the mesiodistal diameter of the M_3 crown at ~10 mm (see above) and continue the curving line from the lateral eminence. This suggests that a small retromolar space was present.

The Palomas 80 immature mandible

The remaining lateral corpus (Figs. 3 and S8) is evenly rounded superoinferiorly, especially by the M_2 , but there is no discrete lateral eminence. It is evenly concave medially below the M_1 . There is no clear mylohyoid line, but there is a modest mylohyoid angle 4 mm below the alveolar plane at the M_1/M_2 . The basilar margin is parallel to the alveolar plane, with slight concavities below the P_4 and M_2 . Posteriorly, there is slight downward turn of the basilar corpus margin, suggesting that the gonial region extended inferiorly of the plane of the basilar margin.

The mental foramen is not preserved on the mandible, but the canal for the inferior alveolar nerve is evident in the anterior corpus break. This indicates that the mental foramen was at least as mesial as the middle of the P_3 .

The anterior margin of the ramus curves up from the distal M_2 , concave anteriorly, with the small opening for the M_3 crypt occurring within the lower portion of that curve. The curve then rises up to become a vertical anterior margin, relative to the alveolar plane. There is an angle of $\sim 136^\circ$ between the concave lower portion and the straight upper portion of the anterior ramus. The coronoid process then angles posteriorly, to reach a peak ~ 29 mm above the alveolar plane. The anterior mandibular notch margin has an even curve down to its lowest point, ~ 14 mm posterior of the coronoid tip, ~ 16 mm anterior of the lingula, ~ 26 mm posterior of the anterior ramus and ~ 35 mm posterior of the distal M_2 , all measurements parallel to the alveolar plane. The mandibular notch is close to parallel to the alveolar plane at its lowest point posteriorly, which should have been close to the condylar neck hence indicating an asymmetrical mandibular notch.

There is modest concavity to the ramus laterally below the anterior mandibular notch. Medially, the endocoronoid crest is well developed. Although the posteroinferior mandibular foramen is not preserved, the lingula is complete, including its posteroinferior edge. The lingula turns strongly medially, and there was no bridging of the mandibular foramen. The tip of the lingula is 23–24-mm posterior of the distal M_2 .

The Palomas 88 immature mandible

The only feature discernible on the Palomas 88 fragment is the position of its mental foramen (see Fig. 3). It is below the distal root of the dm_1 , with its center 11 mm from the alveolar margin.

COMPARATIVE MORPHOLOGY OF THE PALOMAS MANDIBLES

Mandible morphological considerations

It is apparent that the overall proportions and a number of details of the human mandible are the result of its developmental, functional, and spatial conformation to the cranial and pharyngeal regions, in addition to maintaining biomechanical effectiveness for mastication, deglutition, and respiration (Enlow and Hans, 1996). In this context, many, if not most, of the quantitative (both morphometric and discrete trait) attributes used to assess fossil *Homo* mandibles are clearly secondary, if not tertiary, reflections of spatial, developmental, and functional constraints and demands upon the bone (e.g., Trinkaus, 1993; Franciscus and Trinkaus, 1995; Stefan and Trinkaus, 1998b; Rosas, 2001). Yet, thorough assessment of these aspects in the Middle and Late Pleistocene requires associated, mature, nonpathological, facial skeletons essentially complete on at least one side, for which the current fossil record provides nine minimally adequate specimens prior to the Upper Paleolithic. Given the partial preservation and anatomical isolation of the majority of the Late Pleistocene human mandibles, including those from the Sima de las Palomas, the Palomas mandibles are assessed using linear, angular, and cross-sectional morphometrics plus discrete traits, bearing in mind that multiple factors may well determine the affinities of these traits.

MATERIALS AND METHODS

Given the concern with mandibular variability within and across samples, and hence a population approach, the Palomas mandibular remains are compared principally to later Pleistocene human samples that bracket them in time and space. Among late-archaic humans, they are compared to samples of Late-Middle and Late Pleistocene Neandertal remains from western Eurasia (SI-III), given the possible temporal spread of the samples from marine isotope stages (MIS) 5–3. The comparative sample is divided into earlier Neandertal (MIS 6–5) and later Neandertal (MIS 4–3) samples. Comparative data are included for three samples of early modern humans, (1) earlier MIS 6–5 southwest Asian and east African Middle Paleolithic modern humans, (2) penecontemporaneous and slightly younger Early Upper Paleolithic circum-Mediterranean modern humans, and (3) more recent western Eurasian Mid Upper Paleolithic modern humans.

For discrete traits that do not change with age, observations on immature and mature remains are pooled; osteometric comparisons use only mature specimen data for assessment of Palomas 1, 6, 23, and 59, plus an age sequence for morphometric evaluations of Palomas 7 and 49. In the immature mandible osteometric comparisons in which values are plotted against dental ages-at-death, several early adolescent mandibles have been assigned an age-at-death of 12 years even though that represents the lower limits of their probable ages. Despite the ongoing debate concerning Neandertal versus modern human dental developmental rates (Guatelli-Steinberg, 2009), modal recent human dental developmental ages (e.g., Smith, 1991) are used; any distortion in the comparisons from this should be minimal.

The quantitative comparisons include discrete traits that have been noted to occur in high frequencies among the Neandertals (Stefan and Trinkaus, 1998a; Rosas, 2001), a series of standard osteometrics [from or based upon the Martin system (Bräuer, 1988)], and cross-sectional geometric parameters of the mandibular symphysis modeled as a solid beam (cf., Dobson and Trinkaus, 2002). Detailed data for the Palomas mandibles are in Tables S1–S5. The comparative osteometrics and discrete traits are limited to those preserved by the Palomas mandibles.

The symphysis

The mandibular symphysis is preserved for Palomas 23, it is partially present on Palomas 6, and Palomas 1 and 59 retain lateral portions of it (Figs. 1, 2, and 4). The first two mandibles exhibit mentum osseum rank 2 (sloping with a hint of a mental trigone) and the two others exhibit either 2 or 3. It is unlikely that any of them had clear projection of the tuber symphyseos, and hence they are aligned with other Neandertal mandibles and distinct from those of all but two of the early modern human mandibles (Table 1).

Only one of the Palomas mandibles (Palomas 23) provides an anterior symphyseal angle (76°), but the angle for Palomas 6 can be estimated to be between $\sim 75^\circ$ and $\sim 80^\circ$. Comparison of the former to later Pleistocene human distributions (Fig. 5a) places it below the medians of both Neandertal samples and separate from almost all of the early modern humans [only Předmostí 3, with its marked alveolar prognathism, has an angle

TABLE 1. Distributions of mentum osseum ranks (Dobson and Trinkaus, 2002) for the Palomas Neandertals and later Pleistocene comparative samples

Rank	1	2	3	4	5	N
Palomas		75.0%	25.0%			4
Early Neandertal	41.7%	41.7%	16.7%			12
Late Neandertal	13.0%	60.9%	26.1%			23
MPMH		12.5%		87.5%		8
EUP				85.7%	14.3%	7
MUP			3.2%	67.7%	29.0%	31

MPMH, Middle Paleolithic modern humans; EUP, early Upper Paleolithic modern humans; MUP, mid Upper Paleolithic modern humans. Mentum osseum ranks are (1) retreating with no apparent mental trigone; (2) retreating with a clear but nonprojecting mental trigone; (3) largely vertical with a nonprojecting mental trigone; (4) large vertical with a projecting tuber symphyseos but little or no development of the lateral tubercles; (5) prominent tuber symphyseos and lateral tubercles.

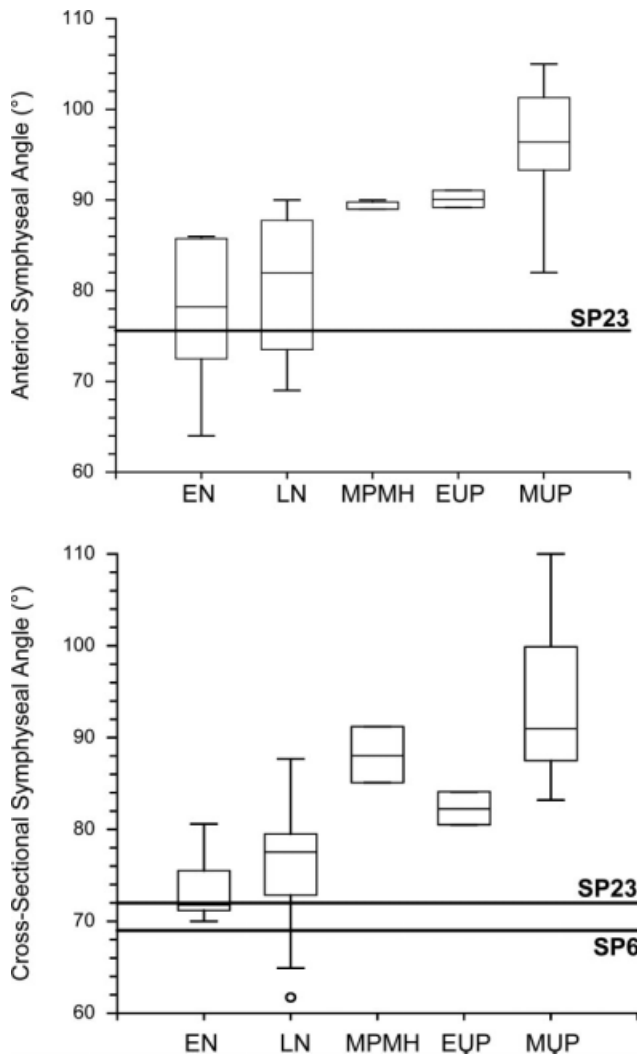


Fig. 5. Box plots of the anterior symphyseal angle (infradentale-pogonion versus alveolar plane) (above) and cross-sectional major axis angle ($I_{\max}$ versus alveolar plane) (below). EN, earlier Neandertals; LN, later Neandertals; MPMH, Middle Paleolithic modern humans; EUP, early Upper Paleolithic modern humans; MUP, mid Upper Paleolithic modern humans; SP23, Palomas 23; SP6, Palomas 6.

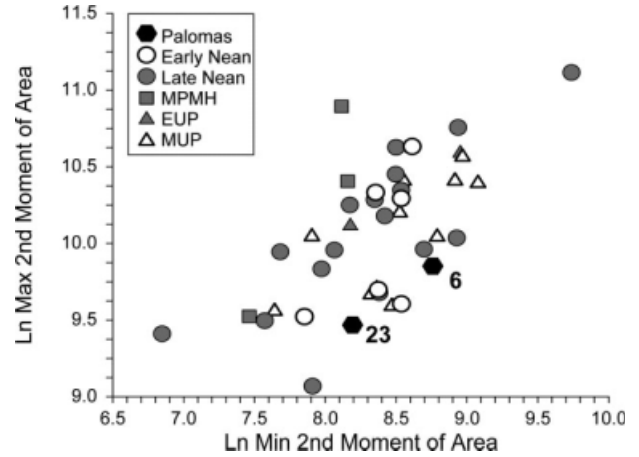


Fig. 6. Bivariate plot of the $\ln_e$ maximum versus minimum second moments of area ($I_{\max}$ vs. $I_{\min}$) of the symphyseal cross-section, modeled as a solid beam, for the Palomas 6 and 23 mandibles and comparative samples. Legend abbreviations as in Figure 5.

<89° among the pooled early modern humans ($N = 18$)). The probable range for the Palomas 6 angle places it similarly among the Neandertals. Comparison of the cross-sectional major axis angle (Fig. 5b) provides similar results. A value for Palomas 6 is provided, because estimation of the missing labial alveoli and possible slight inferior bone loss will have less of an effect on the measurement than it does on the anterior symphyseal angle (cf., Table S2).

The sizes and proportions of the symphysis can be assessed for Palomas 23 and, with estimation, Palomas 6 using geometric parameters of their symphyseal cross-sections (Table S2). The comparison of the maximum (generally, anterosuperior to posteroinferior) second moment of area ($I_{\max}$) to its perpendicular ($I_{\min}$) (see Fig. 6) provides no meaningful separation of the comparative samples; the high $I_{\max}$ Middle Paleolithic modern human outlier is Skhul 4, and the high Neandertal size outlier is Kebara 2. The values for Palomas 6 relative to those of Palomas 23 show its greater overall cross-sectional size (total subperiosteal area of 365 vs. 290 mm²), but both of the Palomas mandibles cluster along the shorter and thicker portion of the later Pleistocene distribution. They are nonetheless close to mandibles from both Neandertal samples and the Mid Upper Paleolithic sample.

The lateral corpus

The lateral corpora of the Palomas mandibles (see Fig. 1) exhibit generally parallel alveolar and basilar margins, nonprominent lateral eminences, and otherwise smooth surfaces. The adult mental foramina are largely below P_4/M_1 and M_1 (all except for the right Palomas 1 foramen and the more distal secondary one of Palomas 23). In this, they are similar to the Neandertal samples, but they are largely distinct from the early modern human samples despite range overlap (Table 2).

The three very young Palomas mandibles (7, 49, and 88) have mental foramina in vicinity of the dm_1 , the most common position for the mental foramen among Neandertals <6 years old (Coqueugnot, 1999). Younger early modern humans have similar positions for the mental foramen (Trinkaus, 2002). However, the older,

TABLE 2. Distributions of mental foramina relative to the dentition for the mature Palomas and comparative sample mandibles

Position	P_3 (%)	P_4 (%)	P_4/M_1 (%)	M_1 (%)	N
Palomas		12.5	50.0	37.5	4
Early Neandertal			45.8	54.2	12
Late Neandertal		11.1	37.0	51.9	27
MPMH		57.1	28.6	14.3	7
EUP		80.0	20.0		5
MUP	10.7	69.6	12.5	7.1	28

The Palomas 23 mental foramen is counted as M_1 , despite the slightly more distal smaller foramen. Sample abbreviations as in Table 1.

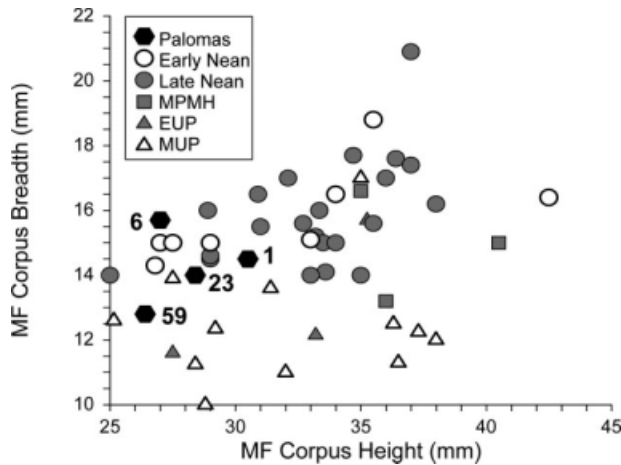


Fig. 7. Bivariate plot of the corpus breadth versus height at the mental foramen for the Palomas 1, 6, 23, and 59 mandibles versus comparative samples. Legend abbreviations as in Figure 5.

early adolescent Palomas 80 mandible has its mental foramen mesial of the P_3/P_4 interdental septum; among immature Neandertals >6 years old, all have the mental foramen at ($N = 1$) or distal ($N = 9$) of the P_3/P_4 septum (Coqueugniot, 1999; Quam et al., 2001). Similarly, all but one (Les Rois 1) of the early modern human mandibles ($N = 12$) in this age range have the mental foramen distal of the P_3 (or dm_1). Palomas 80 therefore has a mesial position for this foramen.

Assessment of adult lateral corpus thickness, using height and breadth at the mental foramen (see Fig. 7) places all four Palomas mandibles at the low end of the later Pleistocene range of variation in height. The Palomas 6 corpus height measurement may be slightly underestimated, given postmortem damage to the bone (see SI), but increases of its corpus height to a maximum of 30 mm would still maintain it among the shorter Neandertal mandibles. There is no significant difference in height across the comparative samples (Kruskal-Wallis $P = 0.295$), but they are significantly different in breadth ($P < 0.001$). None of the Neandertals has a breadth measurement <14.0 mm, and most of the early modern human corpus breadths fall below that value. Three of the Palomas mandibles, 1, 6, and 23, are within the overall Neandertal range. Palomas 1 and 23 are in the lower portion of that distribution, but Palomas 6 remains at the top of the Neandertal range in relative (if not absolute) corpus breadth even with a slight upward

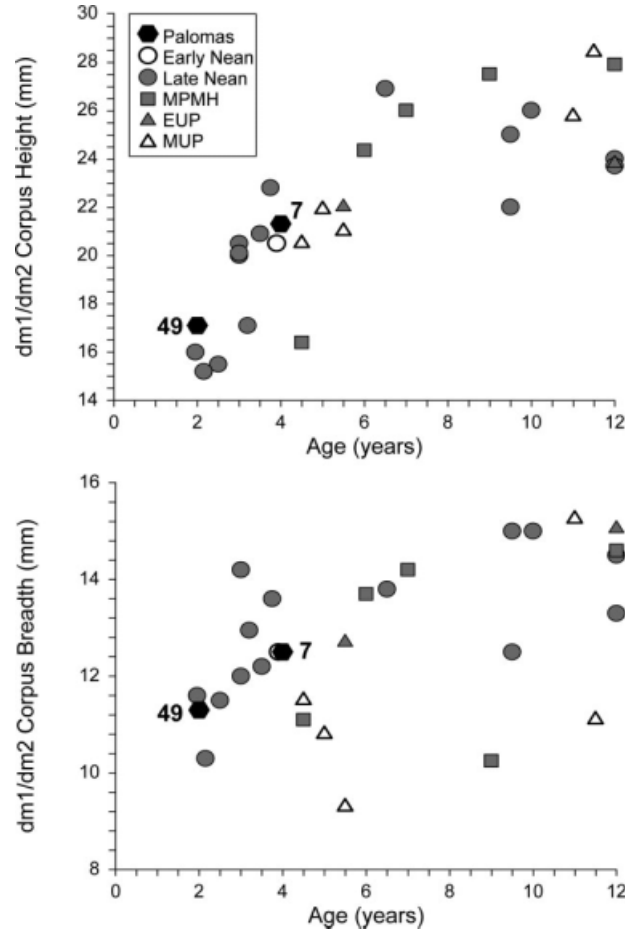


Fig. 8. Bivariate plots of corpus height (above) and breadth (below) at the dm_1/dm_2 (or P_3/P_4) interdental septum for Palomas 7 and 49 and comparative sample immature mandibles. Legend abbreviations as in Figure 5.

adjustment of its corpus height. Palomas 59, however, has the thinnest of these Neandertal mandibular corpora and clusters with the early modern human mandibles in this feature.

Palomas 59 does have among the smallest of the known Neandertal teeth; its M_1 crown breadth (9.5 mm) is 2.51 standard deviations from a Neandertal sample (10.9 ± 0.6 , $N = 48$) and its M_2 breadth (9.3 mm) is 2.25 standard deviations from a similar sample (11.0 ± 0.8 , $N = 37$). However, among Late Pleistocene humans, the individual with the largest molars (Oase 1) has a modest corpus breadth (Trinkaus et al., 2003), and the mandible with the thickest corpus (Kebara 2) has modest molars (Tillier et al., 1989). Least squares regressions of mental foramen corpus breadth against M_1 and M_2 crown breadths across the pooled Late Pleistocene sample, not including the Palomas specimens, produces negative slopes of -0.904 ($N = 36$) and -0.034 ($N = 35$), respectively, neither one of which is significantly different from zero ($P = 0.203$ and $P = 0.954$, respectively). The modest corpus breadth of Palomas 59 is therefore not the result of its small teeth.

Later Pleistocene immature mandible samples are generally similar in corpus height at the dm_1/dm_2 (Fig. 8a), paralleling the nonsignificant difference in corpus height among mature specimens. However,

younger Neandertal immature mandibles tend to have thicker mandibles than similarly aged early modern human ones (Fig. 8b). The two Palomas mandibles providing these corpus measurements, Palomas 7 and 49, fall among these younger Neandertals, although among the more gracile of them. In this relative position, they are similar to the Palomas 1 and 23 adult mandibles but less pronounced than Palomas 6.

The basilar flange

Associated with these corpus characteristics are the basilar flanges present on Palomas 6 and 23 and the incipient form of one on Palomas 7 (Figs. 2 and 3). Palomas 1, 59, and 80 lack them, and their presence on Palomas 49 is equivocal. In a sample of 24 late-adolescent and adult Neandertal mandibles, many of them (62.5%) have a gentle rounded swelling along the infero-lateral mandibular corpus, occasionally with a prominent anterior marginal tubercle, principally below the premolars and mesial molars, with a shallow longitudinal sulcus above it. Yet, all of them have normal digastric impressions, none of them possesses a sharp lateral crest (as in Palomas 6), and none of them has a secondary edge of bone partially fused onto the usual inferior corpus (as in Palomas 23). The prominent part of the flange on Palomas 23 below the P_4 may be an anterior margin tubercle, but the remainder of the flange and its partial separation from the inferior corpus is unknown among other Neandertals. Among the seven Neandertal mandibles between the ages of 2 and 5 years, six (Dederiyeh 1 and 2, Devil's Tower 1, Marsal 1, Molare 1, Pech-de-l'Azé 1) lack the ridge present on Palomas 7, but one (Archi 1) has a similar bony formation (Mallegni and Trinkaus, 1997). None of the immature or mature early modern human mandibles known to us exhibits a similar flange.

The dental arcade

Breadths are provided for the Palomas 23 dental arcade (Table S5) based on a doubling of the distance from the midline to the right side, the midline having been determined from the anterior and posterior symphyseal surfaces. The measurements are therefore approximate. The resultant breadth at the M_1/M_2 (~65 mm) is in the middle of the later Pleistocene ranges of variation (pooled Neandertal samples: 67.3 ± 3.5 mm, $N = 15$; pooled early modern human samples: 64.7 ± 3.6 mm, $N = 14$; t -test; $P = 0.051$; 5 sample ANOVA $P = 0.300$).

Direct breadths can be measured on the Palomas 49 mandible, and they illustrate the broadness of its dental arcade. In the comparison of external bi-dc breadths (Fig. 9a), the younger Neandertals in particular have absolutely wide arcades, and Palomas 49 has the broadest of them. In the more distal arcade, across the dm_2 , there is little difference across the samples, but the Palomas 49 value remains high (Fig. 9b).

The ramus

None of the Palomas mandibles retains a complete ramus, but four of them give indications of their retromolar proportions and two provide discrete traits on their rami.

Palomas 1 exhibits a large retromolar space. Palomas 23 retains the anteroinferior portion of one. It is likely that Palomas 59 possessed a small retromolar space. However, a conservative reconstruction of the distal M_3

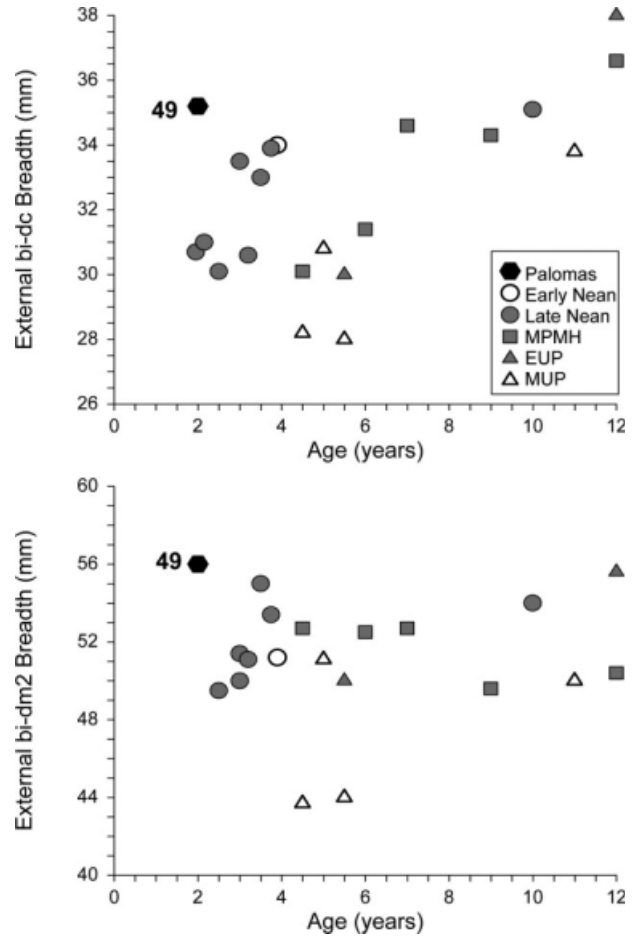


Fig. 9. Bivariate plots of external bi-deciduous canine breadth (above) and external bi-second deciduous molar breadth (below) versus mean dental age for Palomas 49 and immature comparative samples. Legend abbreviations as in Figure 5.

and anterior ramal positions of Palomas 6 indicate that it lacked such a gap in *norma lateralis*. The resultant frequency of 75% is the essentially same as those of the larger Neandertal samples and distinct from the early modern human distributions.

Neandertal rami have been characterized as having relatively straight anterior margins, asymmetrical mandibular notches with the lowest point adjacent to the condylar neck, and a frequent bridging of the mandibular foramen (Kallay, 1970; Smith, 1978; Jidoi et al., 2000; Rak et al., 2002; Table 3). Although variable, the Neandertals tend to have relatively straight anterior rami, but in this they are joined by the Mid Upper Paleolithic sample; Palomas 1 and 80 both have distinct concavities. Most early modern humans have symmetrical mandibular notches, whereas about two-thirds of the Neandertals have the other arrangement. Palomas 1 and 80, although lacking the condylar portion of the notch, are very likely to have had the asymmetrical arrangement. Palomas 80 lacks bridging of the mandibular foramen (horizontal-oval form, lingular bridging), given its projecting lingula. Therefore, in these discrete traits of the ramus, the Palomas mandibles are comfortably within the Neandertal range of variation. At the same time, they exhibit within sample variation, even among those from the stratigraphically later portion of the

TABLE 3. Distributions of mandibular ramal discrete traits, with the more common "Neandertal" configuration designated as "present"

	Retromolar space	Anterior margin straight	Asymmetrical notch	Foramen bridging
Palomas	75.0% (4)	0.0% (2)	100% (2)	0.0% (1)
Early Neandertal	81.8% (11)	57.1% (7)	62.5% (8)	42.3% (13)
Late Neandertal	72.0% (25)	88.9% (18)	66.7% (12)	40.9% (22)
MPMH	42.9% (7)	33.3% (3)	0.0% (4)	0.0% (5)
EUP	0.0% (5)	33.3% (3)	33.3% (3)	16.7% (3)
MUP	18.0% (25)	73.3% (15)	4.1% (24)	0.0% (21)

Percent (N) for each sample.

Sample abbreviations as in Table 1.

Upper Cutting, and some of them do not exhibit all of the more common Neandertal configurations.

DISCUSSION

The Palomas mandibles therefore fall largely within the morphological range of variation of both the earlier and later Neandertal mandible samples, and distinct from early modern humans in a number of characteristics. The principal features that confirm this morphological alignment are their anterior symphyseal configurations, their symphyseal angles (both anterior and cross-sectional), the relatively distal positions of (most of) the mental foramina, the thick lateral corpora of three of the mandibles, the exceptionally wide dental arcade of Palomas 49, the presence of a retromolar space in three of the specimens, and the asymmetrical mandibular notches of Palomas 1 and 80. In the context of MIS 5–3 western Eurasian humans, they align the Palomas mandibles with the Neandertal lineage. As such, they join a suite of cranial, dental, and postcranial features (Walker, 2001; Walker et al., 1998, 2008) in supporting their designation as "Neandertal." Furthermore, given the late age of the specimens from the upper portion of the Upper Cutting (Palomas 49, 59, 80, and 88), they serve to confirm that the late-Middle Paleolithic of Iberia south of the Ebro drainage (cf., Zilhão, 2006) was the product of Neandertals (cf., Walker et al., 2008).

At the same time, Palomas 59 has the thinnest lateral mandibular corpus known for a Neandertal, below the current range of variation and among the values for early modern humans. A shift in facial robusticity has been suggested for the Vindija remains (Smith and Ranyard, 1980; Wolpoff et al., 1981; Janković et al., 2006), and the facial robusticity (if not length) of the male Initial Upper Paleolithic Saint-Césaire 1 is reduced (Lévêque and Vandermeersch, 1980; Trinkaus et al., 1999), although there is little apparent change in the more northern Initial Upper Paleolithic Spy remains (Frapont and Lohest, 1887; Semal et al., 2009).

Palomas 80 has an unusually mesial position of the mental foramen, matched among Neandertal and early modern human late juvenile and adolescent mandibles only by the late-Aurignacian early-modern human Les Rois 1. Mental foramen position, as with retromolar space presence (Franciscus and Trinkaus, 1995) is a complex product of total facial length, dental arcade length, and inferior alveolar nerve canal length (Trinkaus, 1993, 2006). Because most Neandertal facial lengths are similar to, or shorter than, those of earlier *Homo* (Trinkaus, 2003) and their dental arcade lengths are similar to those of most other Pleistocene *Homo* (Franciscus and Trinkaus, 1995), the position of most Neandertal mental foramina below more distal teeth suggests that they

share a shortened inferior alveolar canal length with modern humans.

The more mesial position of the mental foramen in Palomas 80 could therefore reflect either a retained ancestral long canal or, as suggested by Rosas et al. (2006), a reflection of a foreshortened facial length among southern European Neandertals. Palomas 80 is not sufficiently complete to assess its overall dimensions, but visual comparison of it to similarly aged Neandertal mandibles (especially Malarnaud 1 and Teshik-Tash 1) does not imply any reduction in mandibular length. Given preservation, it is not possible to assess whether the other Palomas mandibles exhibit a trend toward facial shortening as suggested by Rosas et al. (2006). However, all of them have relatively low-corpus heights, and the small size or absence of retromolar spaces in Palomas 6 and 59 (despite small teeth in the latter) implies a similar pattern for these Mediterranean Neandertals.

In this context, the significance of the basilar flanges on Palomas 6, 7, and 23 (and Archi 1) is unclear. They do not appear to be pathological. The only muscles inserting in the region are digastric anteroinferiorly and platysma laterally, neither one of which is likely to produce the more posterior portions of the flanges. It is possible that they represent an epigenetic trait (*sensu* Hauser and DeStefano, 1989), in which case they might indicate a close population relationship between these three individuals.

At the same time, there is considerable variation in the mandibles from the Sima de las Palomas, in discrete traits, corpus breadths, and symphyseal morphology. If one assumes that the mandibles found *ex situ* are likely to derive from below the burnt level of the Upper Cutting (see above), the variation is partly within each temporal sample, but also between them. Even though this level of variation is evident in the overall Neandertal sample, the Palomas mandibles emphasizes the degree of variation present within, as well as across, site-specific samples of Neandertals.

CONCLUSION

The Middle Paleolithic of the Sima de las Palomas, Cabezo Gordo, southeastern Spain has yielded four adult and four immature partial mandibles, which help to elucidate the morphological range of both Iberian Neandertals and, for four of the specimens, the mandibular morphology of the latest European Neandertals. In a Late Pleistocene context, they exhibit a suite of ancestral non-modern *Homo* and derived Neandertal mandibular features that serve to distinguish them from early modern humans and align them with other MIS 5–3 Neandertals. Yet, they exhibit considerable morphological

variations, some of which may reflect temporal and/or geographic variation across the Neandertals.

ACKNOWLEDGMENTS

Cabezo Gordo's landowners and the Cabezo Gordo S.A. quarry are thanked for permitting excavation at Sima de las Palomas. The radiographs of the Palomas fossils were made possible by Hospital General Universitario Reina Sofia.

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