New Observations on the Human Fossils from Petit-Puymoyen (Charente)

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ABSTRACT

The site of Petit-Puymoyen has yielded several Neandertal fossils as well as Mousterian stone tools. The anatomy of the PPm1 mandible has been the subject of comment in the past because it has been described as showing a combination of primitive and derived features. Examination of the original fossil confirms the presence of some individual chin elements on the external aspect of the symphysis and superior and inferior transverse tori on the internal aspect. However, this specimen can be comfortably accommodated within the known Neandertal range of variation. Both the PPm1 and PPm3 mandibles show a more modest degree of midfacial prognathism than most Neandertals. In addition, the PPm3 individual possesses a P_3 which shows multiple roots. While a division of the pulp chamber can occasionally be found in Neandertal specimens, complete separation of the roots, as in PPm3, has not been reported in any other Neandertal individual, and represents a primitive feature only rarely found in specimens attributed to the genus *Homo*. A previously unpublished fragment of human occipital bone also was recognized within the sample of human fossils from the site. The presence of unfused sutures and the low thickness values for the bone suggest it represents a late adolescent or young adult individual. The presence of a suprainiac fossa suggests Neandertal affinities for this specimen.

INTRODUCTION

The site of Petit-Puymoyen is located in the region of Charente in southwest France and is well known for its Mousterian deposits (Duport and Vandermeersch 1962; Vandermeersch 1965) and Neandertal remains (Gabis 1956; Piveteau 1957; Siffre 1908). The most complete published inventory of the human remains from the site of Petit-Puymoyen (Vandermeersch 1976) lists six individuals (Table 1). Two fragmentary mandibles and a number of teeth (PPm1–4) were discovered during archaeological excavations carried out at the site in 1907 by A. Favraud (1908). Additional human remains were subsequently discovered by O. Boeuf (1969) during revision of the faunal collection. These include an infant temporal bone (PPm5), recently described by Elyaqtine (1997), as well as a right capitate and left hamate (PPm6) (Oakley et al. 1971). In addition, a left cuboid and left medial cuneiform and two incisors, a right I^2 and unsided I_1, have been reported but never described (Boeuf 1969; Oakley et al. 1971).

During more recent excavations of Petit-Puymoyen, two different areas were established within the site (Du-port and Vandermeersch 1962; Vandermeersch 1965). The first of these is a rock shelter, designated the Abri Commont, which is located in front of the present day cave mouth and whose sediments were covered by large limestone blocks corresponding to the periodic collapse of the cave roof. The second area is represented by the present day cave and corresponds to a narrow 13m long passage. PPm1–4 were recovered from a brecciated level in the rock shelter portion of the site. In contrast, the temporal bone (PPm5) and incisors come from the interior of the cave, while the precise provenience of the hand and foot bones is unknown (Boeuf 1969). The precise age of the deposits is difficult to establish. The faunal remains from the brecciated level are dominated by reindeer, indicating occupation during a cold period, and the stone tool industry has been characterized as somewhat intermediate between the Quina and Ferrassie variants of the Mousterian. The balance of evidence has been interpreted to suggest a late, or even terminal, Mousterian age for the site (Favraud 1908; Vandermeersch 1965), but a precise chronological age for the site remains elusive.

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TABLE 1. INVENTORY OF THE HUMAN REMAINS FROM PETIT-PUYMOYEN.

Inventory No.*	Specimen
PPm 1	Adolescent left mandibular corpus w/P_3-M_2
PPm 2	Adolescent left maxillary fragment w/M^1-M^3
PPm 3	Adolescent right mandibular corpus w/C_1, P_3 and M_1
PPm 4	Right M_2 and M_3
PPm 5	Immature fragmentary right temporal bone
PPm 6	Right capitate and left hamate
PPm 7	Occipital fragment
PPm unnumbered**	Left cuboid, left medial cuneiform, I^2 and I_1

*PPm 1–6 follow Vandermeersch (1976).

**May represent more than one individual.

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The mandibular remains, teeth, and temporal bone (PPm1–5) have been described previously (Elyaqtine 1997; Gabis 1956; Siffre 1908), and the Petit Puymoyen fossils have been frequently included within Neandertal comparative samples in a number of recent studies (Bailey and Hublin 2006; Granat and Heim 2003; Heim and Granat 1995; Mann and Vandermeersch 1997; Manzi and Passarello 1995; Quam et al. 2001; Quam et al. 2009; Spoor et al. 2003; Stefan and Trinkaus 1998a, 1998b). Neandertal affinities have been identified in the dental remains in the morphology of the crown surface (Bailey 2002, 2004; Bailey and Lynch 2005), the accelerated growth rate of the enamel (Ramirez-Rozzi and Bermúdez de Castro 2004), and the patterning of placement of hypoplastic defects (Ogilvie et al. 1989). In addition, the presence of a mastoid fissure and the orientation of the semi-circular canals in the inner ear of the juvenile temporal bone align this specimen with Neandertals (Elyaqtine 1997; Spoor et al. 2003). Regarding the hand bones, the capitate is said to show smaller dimensions while the hamate shows larger dimensions when compared with living humans (Boeuf 1969). In contrast, the anatomical details of the PPm1 mandible have not received much attention of late, but the specimen has been described as showing a derived external symphysis (with chin elements present) and an archaic internal symphysis (with superior and inferior transverse tori present) (Gabis 1956; Piveteau 1957).

Recent examination of the original fossils housed at the Institut de Paleontologie Humaine (IPH) in Paris has revealed a number of anatomical features in the mandibular and dental remains which merit further comment. In addition, the first description of a previously unpublished occipital fragment from this site is presented; it is not included in any published inventory (e.g., Oakley et al. 1971; Vandermeersch 1976), and no mention of its existence can be found in the literature. Nevertheless, its provenience from this site can be confirmed since the name of the site is written in black ink directly on the specimen. This same practice of writing the site name directly on the fossils is also repeated on PPm1–3. In addition, the archives preserved at the IPH contain a reference in 1975 to "*un fragment de voûte crânienne*" within the sample of human fossils from this site housed at the IPH. Thus, we have designated this occipital fragment Petit-Puymoyen 7 (PPm7). It should be noted that a second cranial fragment, corresponding to the right parietal bone in the region of asterion, also is included among the Petit-Puymoyen human remains housed at the IPH. However, the site name is not inscribed on the specimen and it is not mentioned in the 1975 IPH inventory. In addition, the specimen does not preserve any diagnostic features which would help establish its taxonomic status, and there appear to be reasonable doubts as to whether it can be reliably attributed to this site.

PETIT-PUYMOYEN 1

This mandibular fragment preserves part of the left corpus and the symphysis, as well as the P_3–M_2 which are *in situ* within the alveolar sockets (Figure 1). This specimen was described previously (Gabis 1956; Siffre 1908). The left M_2 lacks a distal contact facet and the preserved alveolar bone shows the crypt for the M_3 posteriorly. This suggests the missing M_3 was still in formation. The probable association with the PPm2 maxillary teeth (see below), and the open root apices on the M^3 in the PPm2 maxilla, is also consistent with subadult status. Neandertals have been argued to show a precocious development of the M_3, which are in functional position by around 15 years of age (Wolpoff 1979). Thus, the PPm1 individual would have been younger than 15 years of age at the time of death. A recent study based on the Scladina Neandertal specimen from Belgium (ca 8.0 yrs.) has shown the relative development of the M_3 in Neandertals to be 2–3 years advanced compared with living humans (Smith et al. 2007). The PPm1 individual shows a greater degree of dental calcification than does Scladina since the P_4 is fully occluded and the M_3 is between the R¾-Rc stages in PPm1. Thus, on the whole, the evidence suggests an age at death of between 9–14 years for PPm1, with a more likely estimate falling toward the lower end of this

Figure 1. The Petit-Puymoyen 1 mandible in occlusal (top), left lateral (middle) and symphyseal (bottom) views. Scale=1cm.

age range.

The symphyseal region in PPm1 does show more development of the chin structures than is normally the case in Neandertals, a point made previously (Gabis 1956). There is a slight swelling in the midline which appears to correspond to the symphyseal tubercle and a lateral tubercle is clearly present on the left side of the symphysis toward the basal margin. Just above the lateral tubercle there is a shallow depression, which sets off the tubercle from the surrounding bone. A similar shallow depression is present right of the midline as well. Moving superiorly, these depressions disappear and the bone is inflated. Finally, just below the alveolar margin, the depressions reappear. Thus, this does not appear to represent a mental fossa, since it is divided into a superior and inferior portion by the inflated area in the middle, a condition not commonly seen in modern humans. Nor does there appear to be a mental trigone (contra Gabis 1956), since the symphyseal tubercle is separated from the lateral tubercle by the depression just above it. There is, however, a slight incurvatio mandibulae above the midline swelling. Thus, the PPm1 specimen does not possess a true chin like modern humans, but some of the elements are individually present and weakly expressed in this specimen.

Development of the chin structures is variable among European Neandertal specimens, with some individuals such as La Quina 9 and Guattari 3 showing a relatively pronounced expression of several chin elements. PPm1 resembles La Quina 9 in the presence of the lateral and symphyseal tubercles and the shallow incurvatio mandibulae, but does not show a vertical crest extending superiorly along the midline (Stefan and Trinkaus 1998b). Guattari 3 shows a more pronounced incurvatio mandibulae and presence of a mental trigone (Sergi and Ascenzi 1955). Some variation is present among the late Neandertal mandibles from Vindija. The expression of the external symphyseal features in PPm1 is more pronounced than in Vi 226 and Vi 306, which show a very weak incurvatio mandubulae and no mental trigone (Smith et al. 1985a; Wolpoff et al. 1981). In contrast, the incurvatio mandibulae is clearly more pronounced than PPm1 in Vi 206 and Vi 231, both of which also are described as showing a mental eminence (trigone) (Wolpoff et al. 1981). The external symphyseal morphology in PPm1, then, is within the range of variation documented among European Neandertals.

The symphysis in PPm1 is also fairly vertical, and the angle of the chin with respect to the alveolar plane (85º) is similar to that reported for La Quina 9 (84º) (Stefan and Trinkaus 1998b) and Guattari 3 (88º) (Sergi and Ascenzi 1955). Although the published data for the Vindija mandibles is not directly comparable with PPm1, since the symphyseal angle was measured from the basal plane, the Vindija symphyses are described as approaching the vertical (i.e., ca 90º) with relation to the alveolar plane (Smith et al. 1985a; Wolpoff et al. 1981). Thus, the Vindija symphyses appear more vertical than in PPm1, which is only slightly above the mean value among European Neandertals (81.7º ± 8.1º; n=11) (Stefan and Trinkaus 1998b).

On the internal aspect of the symphysis, moderate superior and inferior transverse tori are present, and this was argued to represent an archaic condition in the PPm1 mandible (Gabis 1956). Along the midline, a shallow genioglossal fossa is present and shows a small foramen in its deepest point. Just lateral of the midline, a sublingual fossa is also present between the two tori. This structure is often found in Neandertals but more rarely in modern humans. Along the basal border of the symphysis, the digastric fossae are oriented posteroinferiorly.

Well-developed internal tori are often found on earlier members of the genus *Homo* (Rightmire 1990; Wood 1991). However, both superior and inferior transverse tori are regularly found in Neandertal mandibles, and the degree of expression of both these structures shows considerable variation, ranging from strongly pronounced (Quam et al. 2001) to nearly absent (Suzuki and Takai 1970). The internal tori in PPm1 are less pronounced than those in Valdegoba 1, which shows well-developed tori (Quam et al. 2001), but seem more similar to the specimens from Vindija and Guattari 2 and 3 (Sergi 1954; Sergi and Ascenzi 1955; Smith et al. 1985a; Wolpoff et al. 1981). Thus, the internal symphysis in PPm1 is archaic in that it is distinguishable from *H. sapiens*, which generally does not show internal tori, but it is clearly within the Neandertal range of variation.

On the lateral aspect of the corpus, the mental foramen is located below the P_4, the anterior marginal tubercle is just slightly posterior to this and the lateral prominence is below the M_2. Neandertal mandibles generally show a more posterior positioning of both the mental foramen (below M_1) and the lateral prominence (below M_3) (Rosas 2001). Only about 11% of European and southwest Asian late Neandertals have a mental foramen placed as far anteriorly as in PPm1 (Walker et al. 2010). In PPm1, both these features are located slightly more anteriorly than the majority of Neandertals, but are still encompassed within the range of variation seen in this Pleistocene population (Rosas 2001; Trinkaus 1993). The placement of the mental foramen in the lower half of the mandibular corpus in PPm1 is a clear indication of its Neandertal affinities, since this appears to be a derived Neandertal condition (Daura et al. 2005).

The posterior placement of the mental foramen in Neandertals has been argued to be due to a shortened inferior alveolar canal length in the context of maintained facial length (Trinkaus 2003, 2006) or related to changes in the size of the tooth row during ontogeny and mesiodistally short premolars (Williams and Krovitz 2004). While the precise reasons behind a more posteriorly placed mental foramen in Neandertals are the subject of ongoing inquiry, a posterior placement of this structure is found even in young Neandertal individuals (Coquegniot 2000), suggesting it is a feature that develops early in ontogeny. In addition, the posterior placement of several of the lateral corpus structures seems to be related to the development of midfacial prognathism in the Neandertal evolutionary lineage (Rosas 2001; Trinkaus 1987). The PPm1 individual, then, appears to have been characterized by a more modest degree of midfacial prognathism than most Neandertals.

The bi-mental foramen breadth in PPm1 (49.0mm) is relatively narrow for a Neandertal, which generally show wide bimental foramen breadths (Daura et al. 2005). Among Neandertals, only the female Tabun 1 specimen (48.0mm) (McCown and Keith 1939) shows a value smaller than in PPm1. This great breadth across the mental foramina appears to be a derived feature in Neandertals and their European middle Pleistocene precursors. It is likely that the large values in Neandertals are related to both the generally more posterior placement of the mental foramen as well as the large dimensions of the crowns and roots of the anterior dentition. The modest value in PPm1 then, is consistent with the somewhat more anterior placement of the mental foramen below the P_4 in this specimen.

Internally, there is a well developed submandibular fossa below the diagonally oriented mylohyoid line. Neandertals are generally characterized by a mylohyoid line which is placed near the alveolar margin at the level of the M_3 and forms the upper boundary of a deep submandibular fossa (Arsuaga et al. 1989; Rosas 2001). The morphology in PPm1 clearly conforms to this condition.

PETIT-PUYMOYEN 3

This is a mandibular fragment preserving the symphysis and part of the right corpus. While the alveolar margin is better preserved, the lower half of the corpus is missing along most of its length. The right C_1, P_3, and M_1, and the roots of right I_1 and I_2 and left I_1, also are preserved. There is only slight wear on the tip of the canine, and the root apices of the P_3 are fully closed. The M_1 shows more wear on the occlusal surface than in PPm1 and a large mesial and small distal interproximal wear facet, indicating the M_2 was in occlusion at the time of death. The probable association with PPm4 (see below) which shows an open apex on the distal root of the M_3, suggests this specimen is just finishing root formation. The degree of dental calcification, then, is slightly advanced compared with the PPm1 mandible. This specimen is more fragmentary than PPm1, but there is a modest superior transverse torus on the internal symphysis and the mental foramen is again placed under the P_4. Both individuals from this site, then, appear to be characterized by less pronounced midfacial prognathism than the majority of Neandertal specimens.

The original description (Siffre 1908) and recent examination of the right P_3 indicate that this tooth shows multiple roots. A groove is evident on the buccal face shortly below the CEJ. Inferiorly, within the broken mandibular corpus, the distal root shows two separate tips (DB and DL), while a third root tip (MB) for the mesial root also is present anteriorly and clearly separated from the other two (Figure 2). This morphology corresponds to the 2R:MB+D category of premolar root form, which is has been argued to represent the primitive condition for the hominin clade (Wood et al. 1988). The PPm3 specimen, then, preserves a very primitive P_3 root morphology only rarely encountered in fossil specimens attributed to the genus *Homo*.

This morphology is present in a few individuals attributed to early members of the genus (Gabunia et al. 2002;

Wood 1991; Wood et al. 1988). In addition, one of the individuals attributed to *H. antecessor* (ATD6-3=Hominin 1) also shows a two-rooted P_3 (Bermúdez de Castro et al. 1999), but a second individual (ATD6-96=Hominin 7) attributed to this taxon apparently lacked this feature (Carbonell et al. 2005). However, the premolar root form (2R:MB+DL) in *H. antecessor* has been argued to represent a derived feature unique to this taxon (Martinón-Torres et al. 2007), and is not the same as that seen in the PPm3 specimen. Among middle Pleistocene specimens, a division of the P_3 root has also been reported in the Arago 13 specimen (Bermúdez de Castro et al. 2003), with each root showing a single canal, but it is nearly absent in the Sima de los Huesos dental sample (Martinón-Torres et al. 2007). Although this feature has not been studied systematically in later Pleistocene hominins, the most common premolar root form would seem to be that of a single root (1R). Among the Neandertals, a division of the P_3 root into lingual and buccal components, corresponding to a Tome's root (2T), occasionally can be found (Kallay 1963; Quam et al. 2001). The root bifurcation seen in the PPm3 specimen has not been previously reported in any other Neandertal specimen.

The functional significance of multiple roots is difficult to identify precisely, but it may be generally related with an increase in tooth crown dimensions (Kovacs 1971). A second individual from Petit-Puymoyen (PPm1) shows no evidence of multiple roots and much smaller P_3 crown dimensions than those in PPm3. These observations suggest that a systematic study of root morphology and crown dimensions in the genus *Homo* is clearly warranted. P_3 root morphology may represent a genetic polymorphism useful for reconstruction of hominin phylogenetic relationships (Bermúdez de Castro et al. 1997; Kupczik et al. 2005), and the root bifurcation seen in the PPm3 specimen would seem to represent a primitive retention in this individual.

PETIT-PUYMOYEN 7

This is an undescribed fragment of the upper portion of the occipital bone, preserving lambda and the medial portions of both right and left lambdatic sutures for articulation with the parietal bones (Figure 3). This suture, then, was not fused at the time of death of this individual. The preserved length of the right lambdoid suture is 24.3mm and the left measures 40.3mm. A small extrasutural ossicle is present at about 17.0mm from lambda along the left side. The occipital fragment shows a maximum ML dimension of 60mm along the lambdoid sutures and a maximum SI dimension of 43.5mm from lambda to the preserved lower margin. The only standard osteometric measurement which can be taken is the bone thickness at lambda (6.5mm).

Comparison with other Pleistocene and recent humans (Table 2) reveals that the value in PPm7 falls below the range of variation in adult fossil *H. sapiens* specimens, although it is probably encompassed within the adult living human range of variation. Compared with adult Neandertals, the value in PPm7 is matched only by that in La Ferrassie 1, and is smaller than the remaining specimens. Bone thickness, however, is clearly greater than in several
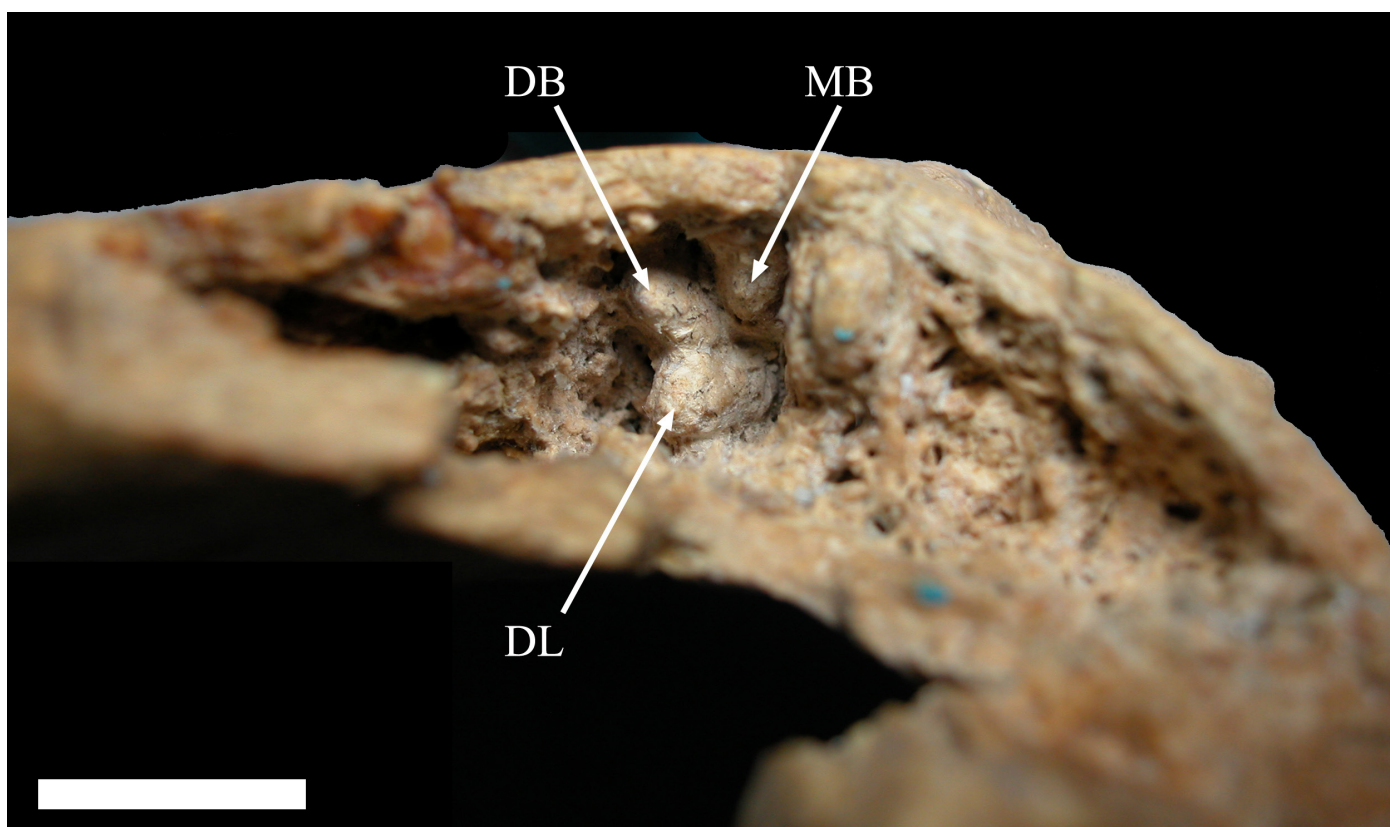
Figure 2. Closeup photograph of the exposed root system in the Petit-Puymoyen 3 mandible, indicating the mesiobuccal (MB), disto-buccal (DB), and distolingual (DL) root tips. Scale=1cm.

immature Upper Pleistocene fossil specimens. This suggests a likely late adolescent/young adult age at death for the PPm7 specimen.

Internally, a portion of the sagittal sinus is preserved (see Figure 3). This curves slightly to the right as it moves inferiorly, and the cerebral fossa is deeper on the right side than the left. This suggests a probable dominance of the right transverse sinus. Externally, the bone is smooth and largely featureless. However, just toward the lowermost preserved margin, a small emissary foramen is preserved near the midline. Slightly inferiorly and lateral to this, a small portion of the suprainiac fossa also is present just left of the midline (see Figure 3 inset). This region shows a slight depression of the bony table and an increase in its rugosity, and its placement corresponds to the location of this structure in Neandertal crania.

The presence of a suprainiac fossa in the PPm7 specimen suggests clear Neandertal affinities since it is a ubiquitous feature among this group of hominins. Although apparently similar areas of bone depression and resorption have been described in specimens that are attributed to modern humans (Frayer et al. 2006; Sofícaru et al. 2007; Trinkaus 2002) as well as even earlier taxa (Trinkaus 2004), this does not appear to be a homologous structure to the suprainiac fossa in Neandertals (Balzeau and Rougier 2010). The early ontogenetic appearance of this feature in Neandertals (Hublin 1980; Madre-Dupouy 1992), as well as its antiquity in the Neandertal evolutionary lineage (Arsuaga

et al. 1997), suggest that its presence in PPm7 is phylogenetically significant and indicates Neandertal affinities for this specimen.

POSSIBLE ASSOCIATIONS
BETWEEN SPECIMENS
Possible associations between the Petit-Puymoyen specimens have been assessed based on the stratigraphic information (when known), repetition of skeletal parts, patterns of tooth wear, and estimated ages at death.

The repetition of skeletal parts in the symphyseal region indicates that the PPm1 and PPm3 specimens represent different individuals. The left maxillary teeth (PPm2) may be associated with PPm1 due to the compatibility in tooth wear. Siffre (1908) argued against this association due to the slightly more advanced dental calcification stage of the maxillary teeth. However, this association also is compatible on stratigraphic grounds since both specimens were found in the rock shelter portion of the site.

The PPm3 right mandibular fragment can be associated with the PPm4 isolated right M_2 and M_3 (Siffre 1908). The mesial wear facet of the M_2 fits very well with the distal face of the M_1 in the mandible. The M_3 shows no wear on the cusp tips, but does show a small, slight wear facet mesially, indicating it was just in occlusion. The distal root shows an open apex, indicating the tooth is just finishing its calcification. Thus, both the articulation between the contact facets and the decreasing degree of molar occlusal wear

Figure 3. The Petit-Puymoyen 7 occipital fragment in endocranial (upper left) and external (upper right) views and detail of the suprainiac region (inset). Note the roughened area of bone surface in the suprainiac area as well as the emissary foramen above it. Scale=2cm. Inset scale=1cm.

moving distally are consistent with these teeth representing the same individual. This association also is compatible on stratigraphic grounds since both specimens were found in the rock shelter portion of the site.

The very young age at death estimated for the PPm5 temporal bone (2–4 years) (Elyaqtine 1997) makes it difficult to associate this specimen with any of the other individuals at the site. Finally, if the presence of open cranial sutures and thickness of the bone in PPm7 are taken to indicate non-adult status, then the occipital fragment could be possibly associated with either of the mandibles from the site.

CONCLUSION

The PPm1 mandible shows a combination of features gen-erally believed to be primitive for the genus *Homo*, a few de-rived Neandertal features, and some features that are more commonly found among *H. sapiens*. Generalized archaic *Homo* features include superior and inferior transverse tori on the internal symphysis, a posteroinferior orientation of the diagastric fossae, a mental foramen located below the P_4 and a lateral prominence below the M_2 on the external corpus, a narrow bi-mental foramen width, and a single-rooted P_3. Derived Neandertal features would include the low position of the mental foramen, a diagonally oriented mylohyoid line and deep submandibular fossa, and the crown morphology of the P_4. The presence of a symphyseal tubercle, incurvatio mandibulae, and anterior and lateral tubercle on the external symphysis are features more commonly found in *H. sapiens* individuals. However, their weak ex-

TABLE 2. BONE THICKNESS MEASUREMENTS (mm) AT LAMBDA IN PPm7 COMPARED WITH PLEISTOCENE AND RECENT HUMANS.

Specimen/Sample	Group	Developmental age (yrs.)	Thickness	Source
Petit-Puymoyen 7			6.5	Present study
La Ferrassie 8	Neandertal	2.5	2.0	(Heim 1982)
La Chaise (Suard)	Neandertal	Child	2.8	(Hublin 1980)
Engis 2	Neandertal	5.0-6.0	4.5	(Hublin 1980)
La Quina H18	Neandertal	8.0	4.3	(Hublin 1980)
Salzgitter-Lebenstedt	Neandertal	Adult	7.3	(Hublin 1984)
Krapina 5	Neandertal	Adult	8.8	(Caspari and Radovčić 2006)
La Chapelle-aux-Saints	Neandertal	Adult	9.0	(Caspari and Radovčić 2006)
La Ferrassie 1	Neandertal	Adult	6.5	(Caspari and Radovčić 2006)
Feldhofer	Neandertal	Adult	9.0	(Caspari and Radovčić 2006)
Spy 1	Neandertal	Adult	10.0	(Vandermeersch 1981)
Spy 2	Neandertal	Adult	8.0	(Caspari and Radovčić 2006)
Tabun 1	Neandertal	Adult	7.0	(Condemi 2001)
Adult Neandertal mean ± s.d. (n)			8.2±1.2 (8)	
Mladeč 3	*H. sapiens*	2.0	1.9	(Teschler-Nicola 2006)
Qafzeh 10	*H. sapiens*	6.0	6.0	(Tillier 1999)
Mladeč 1	*H. sapiens*	c.16.0	5.0	(Teschler-Nicola 2006)
Qafzeh 3	*H. sapiens*	Adult	12.0	(Vandermeersch 1981)
Qafzeh 7	*H. sapiens*	Adult	8.0	(Vandermeersch 1981)
Qafzeh 9	*H. sapiens*	Adult	8.5	(Vandermeersch 1981)
Cro-Magnon 1	*H. sapiens*	Adult	9.0	(Vandermeersch 1981)
Mladeč 5	*H. sapiens*	Adult	7.5	(Teschler-Nicola 2006)
Mladeč 40	*H. sapiens*	Adult?	7.7	(Teschler-Nicola 2006)
Adult fossil *H. sapiens* mean ± s.d. (n)			8.8±1.7 (6)	
Bedouin mean ± s.d. (n)	*H. sapiens*	Adult	7.9±1.7 (11)	(Smith et al. 1985b)
Early Arab mean ± s.d. (n)	*H. sapiens*	Adult	7.4±1.6 (30)	(Smith et al. 1985b)
Hellenistic-Byzantine mean ± s.d. (n)	*H. sapiens*	Adult	6.7±2.1 (16)	(Smith et al. 1985b)
Middle Bronze mean ± s.d. (n)	*H. sapiens*	Adult	7.3±1.7 (11)	(Smith et al. 1985b)
Bedouin mean ± s.d. (n)	*H. sapiens*	Adult	7.5±1.0 (4)	(Smith et al. 1985b)

pression in PPm1 is similar to some other Neandertal specimens as well, and the external symphyseal morphology in PPm1 is within the range of variation documented among European Neandertals. Both the PPm1 and PPm3 individuals, however, do seem to have been characterized by a more modest degree of midfacial prognathism than most Neandertals. The most striking feature in the PPm3 individual is the presence of a primitive root morphology in the P$_3$. This represents a retention of a primitive feature found in early hominins and some early members of the genus *Homo*, but has not been reported previously in any other Neandertal specimen. The PPm7 occipital bone shows low thickness values indicating an adolescent/young adult age at death, and the presence of a suprainiac fossa indicates Neandertal

affinities for this specimen.

Several additional specimens from Petit-Puymoyen have not been assigned inventory numbers (see Table 1), nor studied in detail. Although these specimens were not personally examined, a systematic effort to locate and study all the remaining unpublished specimens from the site is currently ongoing. The recognition of Neandertal affinities in the PPm7 occipital bone suggests that study of the remaining human fossils from the site may also reveal the presence of Neandertal features in these remains. The Petit Puymoyen specimens studied to date further document the Neandertal range of variation in a number of anatomical structures and have revealed new aspects of the paleobiology of Neandertal populations.

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REFERENCES

Arsuaga, J.L., Gracia, A., Martínez, I., Bermúdez de Castro, J.M., Rosas, A., Villaverde, V., and Fumanal, M.P. 1989. The human remains from Cova Negra (Valencia, Spain) and their place in European Pleistocene human evolution. *Journal of Human Evolution* 18: 55–92.

Arsuaga, J.L., Martínez, I., Gracia, A.,and Lorenzo, C. 1997. The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *Journal of Human Evolution* 33(2/3): 219–282.

Bailey, S. 2002. A closer look at Neanderthal postcanine dental morphology: the mandibular dentition. *Anatomical Record (New Anatomy)* 269: 148–156.

Bailey, S. 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. *Journal of Human Evolution* 47: 183–198.

Bailey, S. and Lynch, J. 2005. Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. *American Journal of Physical Anthropology* 126: 268–277.

Bailey, S. and Hublin, J. 2006. Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne). *Journal of Human Evolution* 50: 485–508.

Balzeau, A. and Rougier, H. 2010. Is the suprainiac fossa a Neandertal autapomorphy? A complementary external and internal investigation. *Journal of Human Evolution* 58: 1–22.

Bermúdez de Castro, J., Martinón-Torres, M., Sarmiento, S., and Lozano, M. 2003. Gran Dolina-TD6 versus Sima de los Huesos dental samples from Atapuerca: evidence of discontinuity in the European Pleistocene population. *Journal of Archaeological Science* 30: 1421–1428.

Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M. 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science* 276: 1392–1395.

Bermúdez de Castro, J.M., Rosas, A., and Nicolás, M.E. 1999. Dental remains from Atapuerca-TD6 (Gran Dolina site, Spain). *Journal of Human Evolution* 37: 523–566.

Boeuf, O. 1969. Faune du gisement Moustérien du Petit-Puymoyen. *Bulletin de la Société Archéologique et Historique de la Charente*: 53–128.

Carbonell, E., Bermúdez de Castro, J., Arsuaga, J.L., Allue, E., Bastir, M., Benito, A., Cáceres, I., Canals, T., Díez, J., van der Made, J., Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, J., Rodríguez, X., Rosas, A., Rosell, J., Sala, R., Vallverdú, J., and Vergés, J. 2005. An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *Proceedings of the National Academy of Sciences USA* 102(16): 5674–5678.

Caspari, R. and Radovčić, J. 2006. New reconstruction of Krapina 5, a male Neandertal cranial vault from Krapina, Croatia. *American Journal of Physical Anthropology* 130: 294–307.

Condemi, S. 2001. *Les Néandertaliens de La Chaise*. CTHS, Paris.

Coquegniot, H. 2000. La position du foramen mentonnier chez l'enfant: révision ontogénétique et phylogénétique. *Bulletins et Mémoires de la Société d'Anthropologie de Paris* n.s. t.12(3–4): 227–246.

Daura, J., Sanz, M., Subirá, M., Quam, R., Fullola, J., and Arsuaga, J.L. 2005. A Neandertal mandible from the Cova del Gegant (Sitges, Barcelona, Spain). *Journal of Human Evolution* 49: 56–70.

Duport, L. and Vandermeersch, B. 1962. Le gisement du Petit-Puymoyen. Etude archéologique. *Bulletin de la Société Archéologique et Historique de la Charente* x: 83–105.

Elyaqtine, M. 1997. L'os temporal du Petit-Puymoyen. *Comptes Rendus de l'Académiedes Sciences de Paris* 325: 905–908.

Favraud, A. 1908. La station Moustérienne du Petit-Puymoyen, commun de Puymoyen (Charente). *Revue de l'École d'Anthropologie de Paris* 18: 46–66.

Frayer, D., Jelínek, J., Oliva, M., and Wolpoff, M. 2006. Aurignacian male crania, jaws and teeth from the Mladeč Caves, Moravia, Czech Republic. In: Teschler-Nicola, M. (ed.), *Early Modern Humans at the Moravian Gate: The Mladeč Caves and their Remains*. Springer Verlag, Vienna, pp. 185–272.

Gabis, R. 1956. Etude de la mandibule humaine de la station mousterienne de Petit-Puymoyen (Charente). *Bulletin de la Société géologique de France* 6: 1021–1028.

Gabunia, L., de Lumley, M., Vekua, A., Lordkipanidze, D., and de Lumley, H. 2002. Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *Comptes Rendus Paleovol* 1: 243–253.

Granat, J. and Heim, J.-L. 2003. Nouvelle méthode d'estimation de l'âge dentaire des Néandertaliens. *L'Anthropologie* (Paris) 107: 171–202.

Heim, J.L. 1982. *Les Enfants Neandertaliens de La Ferrassie*. Masson, Paris.

Heim, J.L. and Granat, J. 1995. La mandibule de l'enfant néandertalien de Malarnaud (Ariége). Un nouvelle approche anthropologique par la radiographie et tomodensitométrie. *Anthropologie et Préhistoire* 106: 79–96.

Hublin, J.J. 1980. La Chaise Suard, Engis 2 et La Quina H18: développement de la morphologie occipitale externe chez l'enfant prénéandertalien et néandertalien. *Comptes Rendus de l'Académiedes Sciences de Paris* 291: 669–672.

Hublin, J.J. 1984. The fossil man from Salzgitter-Lebenstedt (FRG) and its place in human evolution during the Pleistocene in Europe. *Zeitschrift für Morphologie und*

Anthropologie 75(1): 45–56.

Kallay, J. 1963. A radiographic study of the Neanderthal teeth from Krapina, Croatia. In: Brothwell, D. (ed.), *Dental Anthropology*. Pergamon Press, Oxford, pp. 75–86.

Kovacs, I. 1971. A systematic description of dental roots. In: Dahlberg, A. (ed.), *Dental Morphology and Evolution*. The University of Chicago Press, Chicago, pp. 211–256.

Kupczik, K., Spoor, F., Pommert, A., and Dean, M. 2005. Premolar root number variation in hominoids: genetic polymorphism vs. functional significance. In: Zadzinska, E. (ed.), *Current Trends in Dental Morphology Research*. University of Lodz Press, Lodz, pp. 257–268.

Madre-Dupouy, M. 1992. *L'enfant du Roc de Marsal: Etude Analytique et Comparative*. CNRS, Paris

Mann, A. and Vandermeersch, B. 1997. An adolescent female Neandertal mandible from Montgaudier cave, Charente, France. *American Journal of Physical Anthropology* 103: 507–527.

Manzi, G. and Passarello, P. 1995. At the archaic/modern boundary of the genus *Homo*: the Neandertals from Grotta Breuil. *Current Anthropology* 36(2): 355–366.

Martinón-Torres, M., Bermúdez de Castro, J., Gómez-Robles, A., Bastir, M., Sarmiento, S., Muela, A., and Arsuaga, J.L. 2007. Gran Dolina-TD6 and Sima de los Huesos dental samples: Preliminary approach to some dental characters of interest for phylogenetic studies. In: Bailey, S. and Hublin, J. (eds.), *Dental Perspectives in Human Evolution State-of-the-Art Research in Dental Paleoanthropology*. Springer, Dordrecht, pp. 65–80.

McCown, T. and Keith, A. 1939. *The Stone Age of Mount Carmel*. Vol. II. *The Fossil Human Remains from the Levalloiso-Mousterian*. Clarendon Press, Oxford.

Oakley, K., Campbell, B., and Molleson, T. 1971. *Catalogue of Fossil Hominids*. Part II: *Europe*. British Museum of Natural History, London.

Ogilvie, M., Curran, B., and Trinkaus, E. 1989. Incidence and patterning of dental enamel hypoplasia among the Neandertals. *American Journal of Physical Anthropology* 79: 25–41.

Piveteau, J. 1957. *Traité de Paléontologie*, VII: *Les Primates*. Masson, Paris.

Quam, R., Arsuaga, J.L., Bermúdez de Castro, J.M., Díez, J.C., Lorenzo, C., Carretero, J.M., García, N.,and Ortega, A. 2001. Human remains from Valdegoba cave (Huérmeces, Burgos, Spain). *Journal of Human Evolution* 41: 385–435.

Quam, R., Bailey, S., and Wood, B. 2009. Evolution of M^1 crown size and cusp proportions in the genus *Homo*. *Journal of Anatomy* 214: 655–670.

Ramirez-Rozzi, F. and Bermúdez de Castro, J. 2004. Surprisingly rapid growth in Neanderthals. *Nature* 428: 936–939.

Rightmire, G.P. 1990. *The Evolution of Homo erectus*. Cambridge University Press, Cambridge.

Rosas, A. 2001. Occurrence of Neandertal features in mandibles from the Atapuerca-SH site. *American Journal of Physical Anthropology* 114: 74–91.

Sergi, S. 1954. La mandibola Neandertaliana Circeo II. *Rivista di Antropologia* 41: 305–344.

Sergi, S. and Ascenzi, A. 1955. La mandibola Neandertaliana Circeo III. *Rivista di Antropologia* 42: 337–403.

Siffre, A. 1908. Étude des dents humaines. *Revue de l'École d'Anthropologie de Paris* 18: 66–72.

Smith, F., Boyd, D., and Malez, M. 1985a. Additional Upper Pleistocene human remains from Vindija Cave, Croatia, Yugoslavia. *American Journal of Physical Anthropology* 68: 375–383.

Smith, P., Wax, Y., Becker, A., and Einy, S. 1985b. Diachronic variation in cranial thickness of Near Eastern populations. *American Journal of Physical Anthropology* 67: 127–133.

Smith, T., Toussaint, M., Reid, D., Olejniczak, A., and Hublin, J. 2007. Rapid dental development in a Middle Paleolithic Belgian Neandertal. *Proceedings of the National Academy of Sciences USA* 104(51): 20220–20225.

Sofícaru, A., Petrea, C., Doboş, A., and Trinkaus, E. 2007. The human cranium from the Peştera Cioclovina Uscată, Romania: Context, age, taphonomy, morphology and paleopathology. *Current Anthropology* 48: 611–619.

Spoor, F., Hublin, J., Braun, M.,and Zonneveld, F. 2003. The bony labyrinth of Neanderthals. *Journal of Human Evolution* 44: 141–165.

Stefan, V. and Trinkaus, E. 1998a. Discrete trait and dental morphometric affinities of the Tabun C2 mandible. *Journal of Human Evolution* 34: 443–468.

Stefan, V. and Trinkaus, E. 1998b. La Quina 9 and Neandertal mandibular variability. *Bulletins et Mémoires de la Société d'Anthropologie de Paris* 10: 293–324.

Suzuki, H. and Takai, F. 1970. *The Amud Man and his Cave Site*. Academic Press of Japan, Tokyo.

Teschler-Nicola, M. (ed.). 2006. *Early Modern Humans at the Moravian Gate*. Springer, New York.

Tillier, A.M. 1999. *Les Enfants Mousteriens de Qafzeh: Interpretation Phylogenetique et Paleoauxologique*. CNRS Editions, Paris.

Trinkaus, E. 1987. The Neandertal face: evolutionary and functional perspectives on a recent hominid face. *Journal of Human Evolution* 16: 429–443.

Trinkaus, E. 1993. Variability in the position of the mandibular mental foramen and the identification of Neandertal apomorphies. *Rivista di Antropologia* 71: 259–274.

Trinkaus, E. 2002. The cranial morphology. In: Zilhao, J. and Trinkaus, E. (eds.), *Portrait of the Artist as a Child The Gravettian Human Skeleton from the Abrigo do Lagar Velho and its Archaeological Context*. Instituto Portugues de Arqueologia, Lisboa, pp. 256–286.

Trinkaus, E. 2003. Neandertal faces were not long; modern human faces are short. *Proceedings of the National Academy of Sciences USA* 100: 8142–8145.

Trinkaus, E. 2004. Eyasi 1 and the suprainiac fossa. *American Journal of Physical Anthropology* 124: 28–32.

Trinkaus, E. 2006. Modern human versus Neandertal evolutionary distinctiveness. *Current Anthropology* 47(4): 597–620.

Vandermeersch, B. 1965. Position stratigraphique et chronologie relative des restes humains du Paléolithique moyen du Sud-Ouest de la France. *Annales de Paléontologie (Vertébrés)* 51(1): 69–126.

Vandermeersch, B. 1976. Les Néandertaliens en Charente. In: De Lumley, H. (ed.), *La Préhistoire Francaise*. CNRS, Paris, pp. 584–587.

Vandermeersch, B. 1981. *Les Hommes Fossiles de Qafzeh (Israel)*. CNRS, Paris.

Walker, M., Lombardi, A., Zapata, J., and Trinkaus, E. 2010. Neandertal mandibles from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. *American Journal of Physical Anthropology* 142(2): 261–272.

Williams, F. and Krovitz, G. 2004. Ontogenetic migration of the mental foramen in Neandertals and modern humans. *Journal of Human Evolution* 47: 199–219.

Wolpoff, M. 1979. The Krapina dental remains. *American Journal of Physical Anthropology* 50: 67–117

Wolpoff, M., Smith, F., Malez, M., Radovcic, J., and Rukavina, D. 1981. Upper Pleistocene human remains from Vindija Cave, Croatia, Yugoslavia. *American Journal of Physical Anthropology* 54: 499–545.

Wood, B., Abbott, S., and Uytterschaut, H. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids IV. Mandibular postcanine root morphology. *Journal of Anatomy* 156: 107–139.

Wood, B. 1991. *Koobi Fora Research Project*. Vol. 4. *Hominid Cranial Remains*. Clarendon Press, Oxford.