



Evolutionary Trends in the Temporal Bone in the Neandertal Lineage: A Comparative Study Between the Sima de los Huesos (Sierra de Atapuerca) and Krapina Samples

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Abstract

A comparative study of the temporal bone in the fossil human collections from the Middle and Upper Pleistocene sites of the Sima de los Huesos (Spain) and Krapina (Croatia), respectively, has revealed a pattern to the emergence of several Neandertal features in the glenoid fossa and mastoid process. The results demonstrate that a flattened articular eminence characterizes the Neandertal evolutionary lineage, and this apparently derived feature is present at least since the time of the Atapuerca (SH) hominids. In contrast, both the size of the postglenoid process and the projection of the mastoid process have clearly undergone a reduction in the Neandertals, including the Krapina sample, from their Middle Pleistocene precursors. The anterior mastoid tubercle is absent in both the Atapuerca (SH) sample and the Krapina hominids, but is ubiquitous in Upper Pleistocene Western European Neandertals, suggesting a later appearance of this feature. Finally, the narrow width of the mastoid process in the Krapina sample appears to be a feature which is particular to this sample.

INTRODUCTION

The first human remains from the Sima de los Huesos (SH) were discovered in the 1970's (1), and systematic excavations have been carried out in the Sierra de Atapuerca over the past 20 years. To date, the site has yielded over 5,000 human fossils, making it the richest human-fossil-bearing site in the world. These remains correspond to a minimum of 28 individuals (2) of both sexes and diverse ages. The site has a firm minimum radiometric age limit of 350 kyr, and probably dates to the interval between 400–600 kyr (3). The SH human fossils have been claimed to be phylogenetically close to the later Neandertals, and have been attributed to the species *Homo heidelbergensis* (4).

The large sample of Neandertal remains from Krapina was recovered during excavations carried out at the turn of the 20th century, and the over 850 human bones recovered from the site make the Krapina collection the largest known Neandertal sample in the world (8–12). Based on the dental remains, a minimum of 35 individuals (Krapina Dental People) have been recognized in the collection (8). With a date

TABLE 1

Samples and specimens included in the present study.

Sample	n	Composition
Recent humans	155	Balanced-sex sample of adult individuals of known sex from Coimbra (Portugal) ^a
Atapuerca (SH)	8	Cranium 1, 4, 5, 8, 12, 13, AT-1592 & AT-124
Krapina ^b	18 ^c	Krapina 3, 5, 10, 38.1, 38.3, 38.5, 38.6, 38.7, 38.9, 38.12, 38.15 38.16, 38.21, 39.1, 39.5, 39.6, 39.7, 39.13 & 39.16
Neandertals	13	Saccopastore 1 & 2, Gibraltar 1, Amud 1, Tabun C1, Shanidar 1, Le Moustier 1, La Chapelle, La Ferrassie 1, La Quina H5, Monte Circeo, Spy 1 & 2
Fossil <i>H. sapiens</i>	12	Predmosti 3 & 4, Dolni Vestonice 3, Mladec 5, Brno 2 & 3, La Chancelade, Qafzeh 9, Skhul 5, Kow Swamp 5, Zhoukoudian Upper Cave C.101 & C.102

^aMale (n=78); Female (n=77)^bNumbering of the Krapina specimens follows their catalog designations (Radović *et al.*, 1988)^cKrapina 38.3 & 39.6 represent the same individual

of c.130 kyr (13), the Krapina hominins predate the bulk of the Western European Neandertal sample.

The Krapina hominins have been broadly compared with the Atapuerca (SH) fossils in previous studies (6, 7, 14–19). The Atapuerca (SH) sample documents an early stage of the Neandertal evolutionary lineage, expressing some Neandertal characteristics in incipient form. On the other hand, the Krapina fossils represent a different stage, at which nearly all the characteristic Neandertal features are expressed. These two large collections provide a rare opportunity to study the degree of biological variation within temporally separated samples of the Neandertal evolutionary lineage and to illuminate the process of the appearance of the characteristic Neandertal anatomy. With this in mind, the present study focuses on a comparison of the anatomy in two regions of the temporal bone, the glenoid fossa and the mastoid region, which have been argued to show characteristic Neandertal features.

MATERIALS AND METHODS

The fossil specimens and samples consulted are presented in Table 1. The Atapuerca (SH) sample includes dozens of temporal bone fragments which correspond to numerous individuals of different ages at death. Most of these specimens have been the object of a prior detailed study (7). The present study includes only the adult specimens in the sample which preserve the glenoid fossa and/or the mastoid process (Table 1). Similarly, among the close to 50 temporal bone fragments in the Krapina collection, we have relied on the adult specimens (8) which preserve these anatomical regions. Data was collected on the original fossil specimens from Krapina and Atapuerca, as well as a number of European Neandertals. In the cases of Shanidar 1, Amud 1, Le Moustier 1, Spy 1 and 2 and Monte Circeo 1, data was collected on high-quality casts of the originals. For some aspects of this study, we have also relied on observations and measurements of the original Broken Hill fossil as well as

high-quality casts of several other African and European Middle Pleistocene specimens.

To compare the samples of Atapuerca (SH), Krapina and the Neandertals we have created two *Homo sapiens* samples. Since both the Krapina and Atapuerca (SH) collections represent closely related and temporally restricted samples of individuals, we have preferred to rely on a large sample of recent humans which share these characteristics. For this reason, we studied a large sample (n = 155) of recent human known-sex adult individuals born between 1820 and 1920 in the Beira litoral region of Portugal, housed at the Instituto de Antropologia of the Universidade de Coimbra. At the same time, since the anatomical variation in our Neandertal sample could be partially due to temporal and geographic differences between specimens, we have constructed a sample of fossil *H. sapiens* which is comprised of individuals of diverse geographic provenience and chronology.

Five metric dimensions and one morphological trait related to anatomical features which are widely cited in studies of Neandertal temporal bones have been considered in this study. The large sample sizes from Krapina and Atapuerca (SH) offer the opportunity to concentrate our metric analysis on a statistical comparison of the samples rather than values of individual specimens. In fact, all of the metric variables show a significant degree of overlap between samples and cannot be used separately to define a species in a strictly cladistic sense, nor to determine whether an isolated specimen belongs to a particular taxon. Nevertheless, they are useful to characterize and understand the evolutionary process at the population level.

Articular eminence angle

The articular eminence of Neandertals has generally been considered to be flatter than in modern humans (20–30). To measure the convexity of the articular eminence, the angle formed by the two slopes of the articular eminence (the anterior wall of the articular fossa and the preglenoid plane) was determined according to the tech-

nique described in Martínez & Arsuaga (7) (Figure 1), which is similar to that of Ashton & Zuckerman (1954). A flatter articular eminence is associated with a higher value for this angle.

Postglenoid process length

The Atapuerca (SH) temporal bones display strongly developed and projecting postglenoid processes (5, 7), and Neandertals also present a well-developed postglenoid process, constituting most of the posterior wall of the articular fossa (21–27, 29, 30). The length of the postglenoid process was directly measured from the deepest point of the articular fossa to its tip (Figure 1). This measurement is not a projection from the Frankfurt horizontal and yields higher values than those of Ashton & Zuckerman (31).

Mastoid process projection

There is a general agreement among researchers that the mastoid processes of Neandertals do not project much below the basicranium (22–25, 29, 30, 32–35). However, this lack of mastoid projection from the basicranium has been attributed to an inflation of the surrounding occipitomastoid region rather than a reduction of the process itself (10, 26–28). The mastoid projection is usually measured from the digastric groove to the tip of the mastoid process, following the technique defined by Zoja (29). Nevertheless, other measures of projection are also possible.

When mastoid projection is measured from the Frankfurt Horizontal, the values in Neandertals are the same as those in modern humans, suggesting no reduction in the size of the mastoid process in Neandertals (28). In contrast, measuring the projection as the vertical distance between the prolongation of the inferior border of the zygomatic process to the tip of the mastoid process (Broca's technique) yields smaller values in Neandertals (30). However, Neandertals appear to have undergone a lowering of the zygomatic process and glenoid cavity relative to the external auditory canal (25, 28, 29, 32, 36). Thus, the smaller values for mastoid projection when measured from the zygomatic process cannot be taken to indicate a reduction in the size of the mastoid process.

Given the importance of this feature and the different results generated by various measurement techniques,

two different measures of mastoid projection have been used in the present study. In addition to the distance from the digastric groove (Zoja's technique), we have also measured the mastoid process projection from the *incisura parietalis* to the apex of the mastoid process, as defined previously (4, 7). This second measure of mastoid projection avoids the problem associated with the relative position of the zygomatic process and external auditory canal in Neandertals and makes it possible to measure isolated and incomplete temporal bones since it is not necessary to orient the fossils.

Width of the mastoid process

The width of the mastoid process is normally measured from the most posterior point of the digastric groove to the most posterior point of the suprameatal triangle according to the technique of Zoja (10, 29). In the present study, we have used a slightly different measurement than that defined by Zoja. Rather than relying on the most posterior point of the digastric groove, we have used the most posterior point of contact between the mastoid process and the digastric groove. Although these two points coincide in many fossil specimens, the most posterior point of the digastric groove sometimes extends well beyond the posterior limit of the mastoid process and may not accurately reflect the width of this structure.

Anterior mastoid tubercle

The presence of an anterior mastoid tubercle has been suggested to represent an autapomorphous (uniquely derived) trait in Neandertals (24, 37–42). Nevertheless, some variation is present in the expression of this feature in both Neandertals and fossil *Homo sapiens* individuals (28, 43). To establish the presence of this trait in the fossils, we have relied on the definition of Hublin (37) of an anterior mastoid tubercle as a distinct tubercle formed by the mastoid crest just behind the external auditory meatus.

RESULTS

The mean values and sample size for each of the metric variables is presented in Table 2. The results for mastoid projection (Zoja) in the Krapina specimens in the present study generally agree with those published previously (10). However, the values for Krapina 3 (6.6 mm), 38.12 (8.1 mm) and 39.1 (7.0 mm), three of the smallest

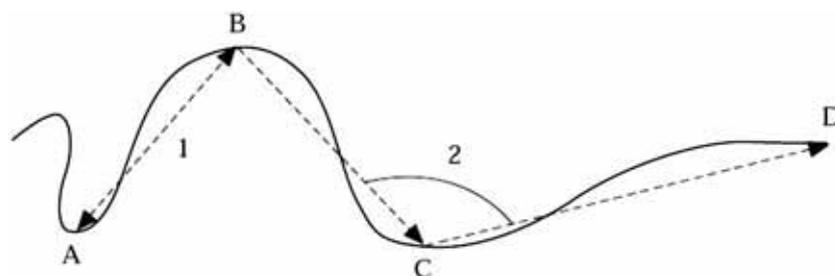


Figure 1. Parasagittal section through the midpoint of the articular fossa. Landmarks: A: Tip of the postglenoid process. B: Deepest point of the glenoid fossa. C: Lowest point of the articular eminence. D: Projection of the crossing point between the infratemporal crest and the sphenotemporal suture. Measurements: 1: Postglenoid process length. 2: Angle of the articular eminence. Higher values in this angle indicate a flatter articular eminence. (7).

TABLE 2

Descriptive statistics for the temporal bone variables in the present study.

Variable	Recent	Fossil	Non-Krapina		Pooled	Atapuerca (SH)
	<i>H. sapiens</i> mean \pm s.d. range (n)	<i>H. sapiens</i> mean \pm s.d. range (n)	Krapina mean \pm s.d. range (n)	Neandertals mean \pm s.d. range (n)	Neandertals mean \pm s.d. range (n)	
Postglenoid process projection (mm)	6.3 \pm 1.7 2.6–11.5 (155)	10.1 \pm 1.9 7.5–13.3 (11)	9.6 \pm 2.7 6.2–15.6 (14)	9.0 \pm 2.2 5.2–13.0 (13)	9.4 \pm 2.5 5.2–15.6 (27)	13.1 \pm 1.7 10.8–15.4 (7)
Articular eminence angle (deg.)	106.5 \pm 10.5 77.7–138.8 (155)	110.5 \pm 9.8 90.6–129.8 (11)	126.1 \pm 6.4 116.6–133.8 (7)	131.3 \pm 6.3 121.0–139.7 (7)	128.7 \pm 6.7 116.6–139.7 (14)	124.0 \pm 8.2 116.2–135.8 (5)
Mastoid projection (Zoja) (mm)	11.8 \pm 2.8 5.1–19.1 (149)	11.7 \pm 2.5 7.8–14.4 (9)	8.8 \pm 1.7 6.6–11.8 (8)	8.2 \pm 2.7 3.4–13.5 (12)	8.4 \pm 2.3 3.4–13.5 (20)	13.2 \pm 3.6 6.7–17.1 (6)
Mastoid projection (Martínez) (mm)	42.6 \pm 5.4 31.5–55.5 (153)	45.3 \pm 6.2 34.7–54.1 (10)	35.9 \pm 4.3 31.1–43.0 (9)	36.8 \pm 4.4 30.9–45.0 (13)	36.4 \pm 4.3 30.9–45.0 (22)	45.1 \pm 4.2 40.0–50.0 (6)
Width of the mastoid process (Zoja) (mm)	22.2 \pm 4.0 12.1–32.0 (146)	28.5 \pm 3.8 22.4–33.0 (9)	21.0 \pm 3.0 16.7–26.6 (9)	25.6 \pm 3.0 19.2–29.3 (12)	23.6 \pm 3.7 16.7–29.3 (21)	27.9 \pm 2.9 23.0–31.4 (6)

specimens, are significantly larger in the present study. This difference may be due to the distinct morphology of the digastric groove in the Krapina specimens and other Neandertals, who show an elevation of the anterior floor (7, 29, 30, 42, 44, 45). Since one of the measurement points in Zoja's technique is the floor of the digastric groove, a slight difference in the location of the measurement point may result in different values for mastoid projection.

Regarding the values for the width of the mastoid process, the slightly different measurement technique used in the present study yields slightly smaller values for mastoid width. Comparing the measurements we obtained in the seven Krapina specimens also measured by Smith (1980), the mean value in the present study (21.9 mm) is slightly narrower than that of Smith (10) (24.1 mm).

In four of the five metric variables (postglenoid process length, angle of the articular eminence, and both measures of mastoid projection), no statistically significant difference was detected between the Krapina sample mean value and that of the remaining Neandertal specimens (Table 3), underlining the anatomical similarity of these features within the Neandertal population. For these four variables, the Krapina specimens were grouped together with the remaining Neandertals in a single, pooled Neandertal sample for comparative purposes (Tables 2 & 4).

Glenoid fossa

The pooled Neandertal sample (Tables 2 & 4) shows a postglenoid process which is significantly smaller than that in the Atapuerca (SH) sample, but significantly larger than Coimbra, and similar in size to the fossil *H. sapiens* sample. The postglenoid process is very large in the Atapuerca (SH) sample, and a well-developed postglenoid process is also seen in other European Middle Pleistocene specimens from Steinheim (12.4 mm) and

TABLE 3

Results of the t-test (p value) for differences* between sample means in the Neandertal lineage.

Variable	Atapuerca (SH)	Krapina
Postglenoid process projection		
Krapina	0.007	
Neandertals	0.001	0.553
Articular eminence angle		
Krapina	0.628	
Neandertals	0.110	0.149
Mastoid process projection (Zoja)		
Krapina	0.010	
Neandertals	0.005	0.615
Mastoid process projection (from <i>incisura parietalis</i>)		
Krapina	0.001	
Neandertals	0.001	0.659
Width of the mastoid process (Zoja)		
Krapina	0.001	
Neandertals	0.132	0.003

*We have used a significance level of $p < 0.05$

Petralona (13.0 mm) and has been reported to characterize both Castel di Guido (46) and Reilingen (47). This suggests that a very well-developed process is the common condition in the European Middle Pleistocene, from which the Neandertals, including Krapina, appear to have reduced the size of their postglenoid process.

Among African Middle Pleistocene specimens, postglenoid size ranges from large (Broken Hill = 12.4 mm; Omo 2 = 10.8 mm) to small (LH 18 = 6.8 mm; Ndutu

TABLE 4

Results of the t-test (p value) for differences* between sample means.

Variable	Coimbra	Fossil <i>H. sapiens</i>	Neandertals	Atapuerca (SH)
Postglenoid process projection				
Fossil <i>H. sapiens</i>	0.000			
Neandertals	0.000	0.342		
Atapuerca (SH)	0.000	0.004	0.001	
Articular eminence angle				
Fossil <i>H. sapiens</i>	0.216			
Neandertals	0.000	0.000		
Atapuerca (SH)	0.000	0.019	0.217	
Mastoid process projection (Zoja)				
Fossil <i>H. sapiens</i>	0.964			
Neandertals	0.000	0.002		
Atapuerca (SH)	0.222	0.366	0.001	
Mastoid process projection (from incisura parietalis)				
Fossil <i>H. sapiens</i>	0.126			
Neandertals	0.000	0.000		
Atapuerca (SH)	0.262	0.940	0.000	
Width of the mastoid process (Zoja)				
Fossil <i>H. sapiens</i>	0.000			
Neandertals	0.134	0.003		
Atapuerca (SH)	0.001	0.764	0.395	
Krapina	0.360	0.000	0.015	0.001

The Neandertal sample includes the Krapina specimens for all variables except the width of the mastoid process, where the Krapina sample differs significantly from the remaining Neandertals

*We have used a significance level of $p < 0.05$

= 5.1 mm). Although this sample is too small to establish its statistical significance, the mean value (8.8 mm) is more than 1.5 s.d. above the Coimbra mean but much closer (0.7 s.d. below) to the fossil *H. sapiens* mean. This suggests a parallel trend toward postglenoid reduction has also occurred in the *H. sapiens* evolutionary lineage and the presence of a similarly sized postglenoid process in both Neandertals and fossil *H. sapiens* (Table 2) may represent a case of parallelism.

The values for the articular eminence angle show significant differences between the Neandertal lineage samples (higher angles) and those of fossil and recent *H. sapiens* (lower angles) (Tables 2 & 4). This confirms previous suggestions of a characteristically flat articular eminence in Neandertals. This flat articular eminence is also present in the Atapuerca (SH) sample (7) and Steinheim (131°). It also appears to be present, from published photographs and drawings, in other European Middle Pleistocene specimens, such as Castel di Guido (46), Reilingen (47) and Bilzingsleben (48).

In contrast, African Middle Pleistocene specimens show more raised articular eminences and lower angles (Broken Hill = 109.6°; Omo 2 = 111.7°; Nduku = 116.9°; Laetoli H18 = 123.8°). The mean value for this small

sample (115.5°) is within one s.d. of the mean value in both fossil and living *H. sapiens*, but further from the means in the Neandertal lineage samples.

It is clear that a flat articular eminence is a feature which characterizes the Neandertal lineage from at least Middle Pleistocene times. Other researchers have also found distinctions in the glenoid cavity (32, 49) and mandible (50) of Neandertals, which may be related to a masticatory specialization within this evolutionary lineage (50).

Mastoid region

The values for projection of the mastoid process are significantly smaller in the Neandertal samples than those in the Atapuerca (SH) and fossil and recent *H. sapiens* samples (Tables 2–4). This is true regardless of whether the projection is measured from the floor of the digastric groove (Zoja's technique) or from the *incisura parietalis*, confirming the presence of small mastoid processes in Neandertals.

It is noteworthy that the mastoid processes in the Atapuerca (SH) sample are as projecting as in the *H. sapiens* samples. This could suggest that a projecting mas-

toid process is the ancestral condition in both the Neandertal and *H. sapiens* evolutionary lineages. This idea is reinforced by the presence of well-projecting mastoid processes in African Middle Pleistocene specimens. The mean value of this sample (Broken Hill, Nduetu, Omo 1 & 2 and Laetoli H18) for the projection of Zoja (10.8 mm) is slightly more than one s.d. above the pooled Neandertal sample mean (Table 2), but within one s.d. of the Atapuerca (SH) and *H. sapiens* samples. Relying on the second measure of mastoid projection, from the *incisura parietalis*, the African Middle Pleistocene mean (43.5 mm) is 1.6 s.d. above the pooled Neandertal mean, but well within one s.d. of the Atapuerca (SH) and *H. sapiens* samples.

In light of this, it is interesting to note (Figure 2) that the immature individuals from Atapuerca (SH) show values for both measures of mastoid projection [Zoja ($n=4$) = 8.4 mm; from *incisura parietalis* ($n=3$) = 32.9 mm] that are well below those in the adult specimens from this same site, but very similar to the pooled Neandertal mean values. This suggests that the Neandertals retain the juvenile condition from their Middle Pleistocene precursors (5) and that this is a derived trait in the Neandertals.

The width of the mastoid process is the only variable which showed significant differences between the Krapina sample and the remaining Neandertals, being narrower in Krapina (Table 3). In contrast, the mean values in the Atapuerca (SH), non-Krapina Neandertals and fossil *H. sapiens* do not differ statistically, highlighting this peculiarity in the Krapina sample.

This result could be interpreted as being consistent with the hypothesis of an over-representation of females in the Krapina sample (51), since living populations show sexual dimorphism in their mastoid width. In fact, in our living human sample from Coimbra, the difference between sexes in mastoid width (male mean = 26.1 ± 3.41 mm; female mean = 24.0 ± 2.95 mm) is significant ($p < 0.001$) (Martínez, 1995).

However, previous morphological (10) and metric (52) studies of the temporal bone, focusing specifically on the mastoid process, in the Krapina sample have not found a systematic bias toward females. Moreover, if a bias toward females were present in the Krapina temporal bone sample, this would also have been reflected in the mastoid projection, something which was not found in this study. Thus, we believe that a narrow mastoid process represents a peculiar feature of the Krapina sample, within Neandertals.

The presence of an anterior mastoid tubercle is the single morphological character considered in the present study (Table 5). An anterior mastoid tubercle (*sensu* Hublin, 37) was not found in any specimen from the Atapuerca (SH) (Figure 2), fossil *H. sapiens* or Coimbra samples. Nor is this feature present in any of the Krapina specimens. This observation coincides with that of Frayer (43), but differs from Santa Luca (40) who reported its presence in Krapina 3 (but see Figure 2). Outside of

TABLE 5

Frequency of the anterior mastoid tubercle.

Specimen/Sample	n	Present	Absent
Saccopastore 1			X
Saccopastore 2			X
Gibraltar 1			X
La Ferrassie 1		X	
La Chapelle-aux-Saints		X	
La Quina H5		X	
La Quina H18		X	
Monte Circeo 1		X	
Spy 1		X	
Spy 2		X	
Amud 1			?
Tabun C1			X
Atapuerca (SH)	8	0	8
Krapina	12	0	12
Fossil <i>H. sapiens</i>	12	0	12
Recent <i>H. sapiens</i>	155	0	155

Krapina, there appear to be two clear Neandertal groups. The anterior mastoid tubercle is also absent in both crania from Saccopastore (although Condemi (25) says it is present on the right side of Saccopastore 1), which are of a similar chronology as the Krapina site. Interestingly, this is also the case in Gibraltar 1. At the same time, this tubercle is ubiquitous among later Western European Neandertals. This could indicate that the anterior mastoid tubercle is a feature which appears at a later stage in the Neandertal evolutionary lineage.

In light of this, the expression of this feature in the Neandertals from Southwest Asia is very interesting. This feature is not seen in Tabun C1, the oldest Neandertal specimen from this region, and according to Trinkaus (28), it is also absent in Shanidar 2 and 5. Shanidar 1 (28) and Amud 1 show a swelling on the superoanterior surface of the mastoid process, but no true anterior mastoid tubercle (*sensu* Hublin, 37). In our opinion, the Southwest Asian Neandertals express the archaic condition (i.e. absence or very low frequency of the anterior mastoid tubercle) seen in earlier specimens from European sites, which could indicate an early split within the Neandertal evolutionary lineage between the two (European and Southwest Asian) populations, as has been suggested previously (25, 42).

CONCLUSIONS

The comparison between the two large, temporally separated, samples from Atapuerca (SH) and Krapina has revealed a pattern to the appearance of several characteristic features in the glenoid fossa and mastoid region of the Neandertal temporal bone. The derived flat articular eminence of the Neandertals appears early in this

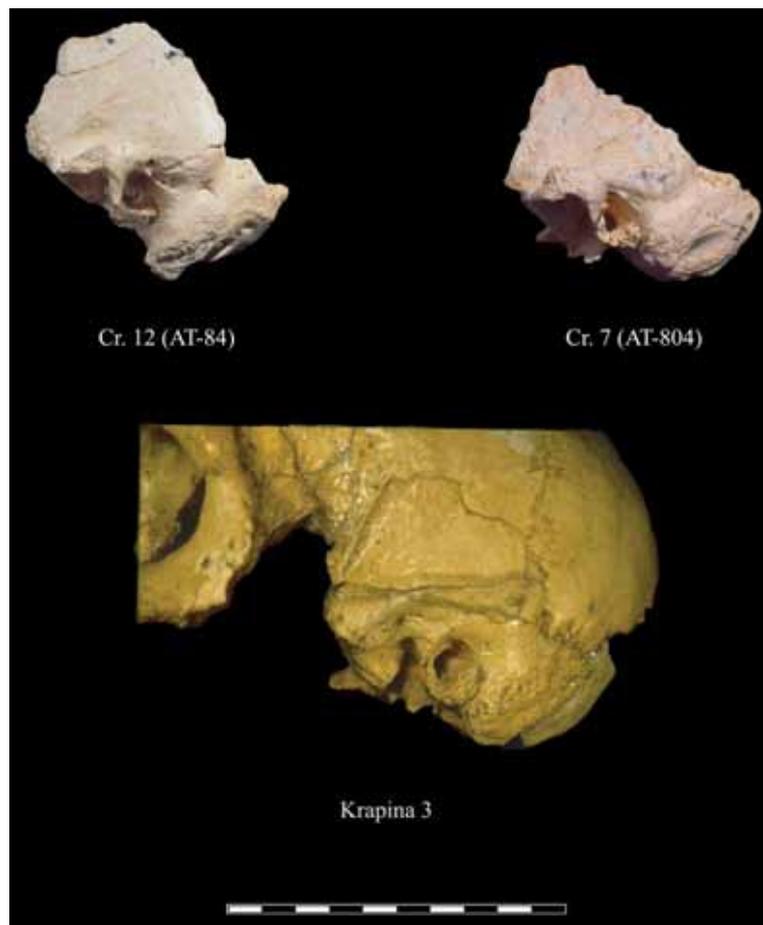


Figure 2. Temporal bones from adult (Cr. 12) and juvenile (Cr. 7) individuals from Atapuerca (SH) and Krapina 3 (reversed). Note the absence of an anterior mastoid tubercle on all three specimens, in which the mastoid crest runs obliquely toward the tip of the mastoid process well behind the external auditory canal. The size and projection of the mastoid process in the juvenile Cranium 7 from Atapuerca (SH) resembles that seen in the adult Neandertal specimen Krapina 3.

evolutionary lineage and was already present in their European Middle Pleistocene precursors. This is the first derived Neandertal feature to appear in the temporal bone and appears to characterize the entire Neandertal evolutionary lineage, being present in some of its earliest members.

In contrast, there is a trend toward reduction of the postglenoid process from the very large examples in the Atapuerca (SH) sample, and other European Middle Pleistocene specimens, to the more reduced sizes in the Neandertals. Nevertheless, the size of this structure in Neandertals remained quite large compared with living humans.

Similarly, the projection of the mastoid process has clearly reduced in the Neandertals, regardless of how this is measured, from the well-projecting mastoid processes in the Atapuerca (SH) sample. In this aspect, adult Neandertal anatomy is similar to that seen in the juvenile individuals of their evolutionary precursors. In Krapina, both the postglenoid process and the projection of the mastoid process have already reached Neandertal-like proportions, and no statistical difference was detected

between the Krapina sample and other non-Krapina Neandertals, suggesting this reduction occurred sometime during the Middle Pleistocene after the time represented by the Atapuerca (SH) sample.

A narrow mastoid process in the Krapina sample distinguishes it from both the Atapuerca (SH) sample and the non-Krapina Neandertals. This appears to be a peculiar feature of the Krapina hominids since the mastoid projection was similar to the rest of the Neandertals included in this study, and may reflect a close biological relationship between the individuals which comprise the Krapina sample. Finally, the absence of an anterior mastoid tubercle in the Atapuerca (SH) sample, the Krapina specimens, and other early European Neandertals, suggests this trait appears at a later evolutionary stage in this lineage.

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