

Human hyoid bones from the middle Pleistocene site of the Sima de los Huesos (Sierra de Atapuerca, Spain)

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Abstract

This study describes and compares two hyoid bones from the middle Pleistocene site of the Sima de los Huesos in the Sierra de Atapuerca (Spain). The Atapuerca SH hyoids are humanlike in both their morphology and dimensions, and they clearly differ from the hyoid bones of chimpanzees and *Australopithecus afarensis*. Their comparison with the Neandertal specimens Kebara 2 and SDR-034 makes it possible to begin to approach the question of temporal variation and sexual dimorphism in this bone in fossil humans. The results presented here show that the degree of metric and anatomical variation in the fossil sample was similar in magnitude and kind to living humans. Modern hyoid morphology was present by at least 530 kya and appears to represent a shared derived feature of the modern human and Neandertal evolutionary lineages inherited from their last common ancestor.

Keywords: Atapuerca; *Homo heidelbergensis*; Hyoid bone; Middle Pleistocene; Sima de los Huesos

Introduction

The hyoid bone is one of the least represented skeletal elements in the human fossil record, and the recent discovery of an *Australopithecus afarensis* hyoid bone (Alemseged et al., 2006), reported as being chimpanzee-like, has generated renewed interest in the evolutionary significance of this bone in the human lineage. Previously, only two hyoids from the genus *Homo* were known: the Kebara 2 Neandertal specimen (Arensburg et al., 1989, 1990; Arensburg, 1991) and the Neandertal hyoid body

SDR-034 (Rodríguez et al., 2003) from the site of El Sidrón cave (Asturias, Spain), dated to around 43 ka (Rosas et al., 2006).

Both Neandertal specimens are modern-human-like in size and shape (Arensburg et al., 1989; Rodríguez et al., 2003). Based on the Kebara 2 hyoid, it was proposed that the position, form, size, and relationship of this bone with the Neandertal larynx was also modern-human-like and that, consequently, these fossil humans had the capacity for spoken language (Arensburg et al., 1989, 1990). Other researchers have contested this conclusion, arguing that neither the dimensions nor the morphology of the hyoid bone were direct indicators of the position of the larynx in the throat (Lieberman et al., 1992). On the other hand, the chimpanzee-like bulla-shaped hyoid bone of *A. afarensis* has been suggested to be consistent with the presence of laryngeal air sacs in this hominin species

(Alemseged et al., 2006), a primitive feature of apes including chimpanzees but not present in modern humans (Aiello and Dean, 1990; Nishimura et al., 2006).

The chimpanzee-like anatomy of the hyoid appears to represent the primitive hominin condition, and its presence in *A. afarensis* indicates that the derived modern human morphology emerged at some point during the course of human evolutionary history. The presence of a human-like hyoid in the Neandertal specimens Kebara 2 and SDR-034 suggests that this derived condition was also present in the last common ancestor of the Neandertal and modern human evolutionary lineages. In this context, the two human hyoid bones recovered from the middle Pleistocene site of the Sima de los Huesos in the Sierra de Atapuerca in northern Spain are particularly relevant, because they considerably extend the known fossil record for the genus *Homo* to deep in the middle Pleistocene and can help elucidate when the derived hyoid morphology first emerged in the human lineage.

Materials and methods

The Sierra de Atapuerca is well known for both the extraordinarily large sample of middle Pleistocene human fossils recovered from the site of the Sima de los Huesos (Arsuaga et al., 1993; Arsuaga et al., 1997a) and for the discovery of some of the oldest human fossils in Europe in the lower Pleistocene beds of the Gran Dolina site (Carbonell et al., 1995; Bermúdez de Castro et al., 1997). The Sima de los Huesos (SH) site is at the foot of a 13-m-deep shaft placed deep inside a cave (Cueva Mayor) located on the southern slope of the Sierra de Atapuerca. Prior to the 2006 field season, the SH site has yielded more than 5,500 human fossils, belonging to at least 28 individuals (Bermúdez de Castro et al., 2004), which have been assigned to the species *Homo heidelbergensis* and are considered to represent the ancestral European population that evolved into the Neandertals (Arsuaga et al., 1997b; Martínez and Arsuaga, 1997). The SH site has a firm minimum radiometric age of 530 ka (Bischoff et al., 2007). The two hyoid bones described here were recovered in 1994 (AT-1500) and 1997 (AT-2000).

To compare the main metric dimensions of the SH fossils, we have relied on a mixed-sex sample of modern humans in the Hamann-Todd Osteological Collection housed at the Cleveland Museum of Natural History (USA). This sample consists of 60 individuals, 34 African-Americans (22 males and 12 females) and 26 European-Americans (23 males and 3 females). This sample size is equivalent to that used by Arensburg et al. (1989), but it shows less temporal heterogeneity and a lower degree of variation. We have also relied on a small sample of 17 modern human hyoid bones for the morphological comparisons. Seven of these derive from cadaveric dissection of male individuals at the School of Medicine at the Universidad Autónoma in Madrid, and the remaining ten, of unknown sex, were recovered during systematic excavations of a medieval Spanish cemetery from the San Pablo monastery in Burgos, Spain (Adán-Álvarez, 2003). We have also had the

opportunity to study the original hyoid of Kebara 2, housed in the Department of Anatomy and Anthropology at Tel Aviv University. The main metric dimensions and anatomical details of the hyoid body SDR-034 have been published previously (Rodríguez et al., 2003). We have measured the same variables in the two SH individuals and the modern human sample as those defined previously by Arensburg et al. (1989) (Table 1).

The Atapuerca (SH) hyoid bones

AT-1500

This specimen is a nearly complete hyoid body that shows only slight loss of the external table of bone, particularly in the region of the anterior tubercle and in the area of articulation between the body and the right greater horn (Fig. 1). However, most of the articular surfaces between the body and the greater horns are preserved, and their presence implies that the greater horns had not yet fused to the body. The superior and the inferior borders are completely preserved, and the body shows a modern-human-like profile in lateral view that is clearly different from the bulla shape found in chimpanzees or the DIK-1-1 specimen.

In ventral view, the hyoid body has a subquadrangular shape, with the transverse (mediolateral) width being greatest at the level of the superior border. The ventral aspect has a very strong anterior tubercle on the midline. On both sides of this tubercle, two marked depressions are present in the region of the insertion of the geniohyoid muscles. The ventral surface does not extend to any great degree below the anterior tubercle. The dorsal aspect does not have the bulla shape characteristic of chimpanzees; rather, it is smoothly concave, similar to modern human hyoids. Nevertheless, a moderate and well-delimited circular depression some 8 mm in diameter is present in the center of the dorsal aspect. Finally, the superior border has a V-shaped contour in superior view.

Table 1
Measurement definitions for the hyoid body

Measurement	Definition
Maximum medial height	Maximum distance from the upper to the lower borders of the body along the sagittal plane.
Maximum transverse diameter	Maximum diameter of the body taken in the transverse (ML) plane.
Anteroposterior thickness	Direct distance between a line joining the upper and the lower posterior margins of the body at the midline, and the most protruding anteromedial point on the ventral aspect.
Depth of the posterior surface	Measured from a line joining the upper and the lower posterior margins of the body in the sagittal plane to the most anteromedial point on the dorsal aspect.
Thickness of the inferior border	Measured in the sagittal plane of the inferior border.

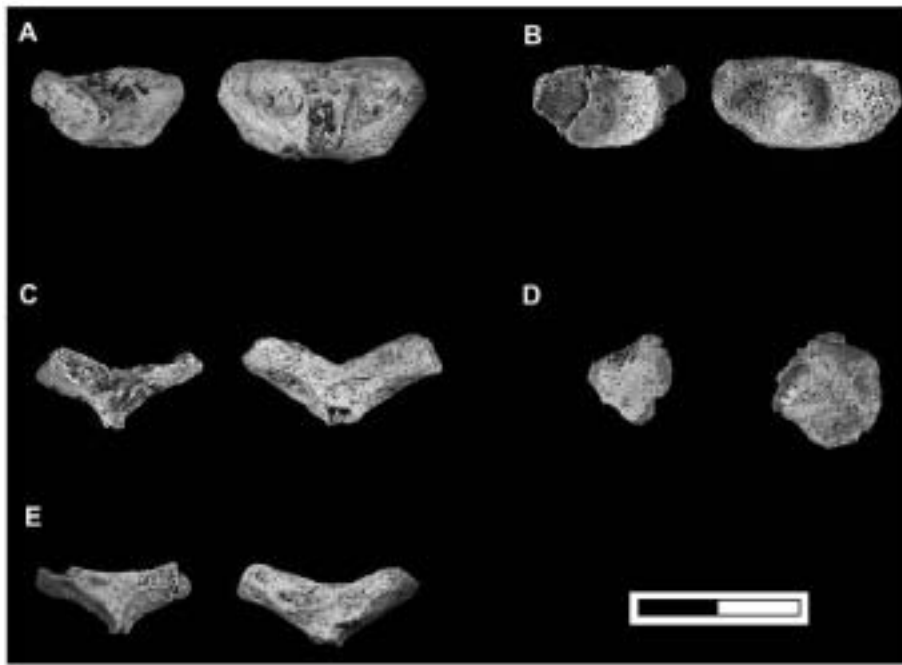


Fig. 1. The AT-2000 (left) and AT-1500 (right) Sima de los Huesos hyoid bones in ventral (A), dorsal (B), superior (C), lateral (left side) (D), and inferior views (E). Scale bar = 2 cm.

AT-2000

This specimen consists of most of a hyoid body characterized by more extensive loss of the external table than in AT-1500, mainly in the left portion of the dorsal aspect, along the superior border, and in the right region of the ventral aspect next to the articulation with the greater horns (Fig. 1). In spite of this erosion, part or most of the articular surface with the greater horns is preserved on both sides, suggesting, as in the case of AT-1500, that the greater horns had not yet fused to the body. In addition, the presence of the articular surfaces for the greater horns indicates that the slight erosion present along the superior border did not significantly alter the original size and shape of the body. As in AT-1500, the lateral profile is modern-human-like.

The body of AT-2000 has a subquadrangular shape in ventral view, with the transverse width along the superior border being greater than that along the inferior border. A marked anterior tubercle—smaller than that in AT-1500—is visible near the midline. In contrast to AT-1500, there are no fossae on either side of the tubercle for the insertion of the geniohyoid muscles in AT-2000. In the better preserved left lateral portion of the ventral aspect, below the anterior tubercle, three small fossae can be distinguished at the insertion sites for the thyrohyoid, omohyoid, and sternohyoid muscles. The inferior border of AT-2000 is completely preserved along its midline and is somewhat thinner than that of AT-1500.

The dorsal aspect of AT-2000 is not bulla-like, but is regularly concave, as is the case in AT-1500. However, there is no well-delimited circular depression as in AT-1500. In superior view, the contour of AT-2000 is more open, or horseshoe-shaped, than in AT-1500, and it does not show the marked apex that characterizes the V-shape in AT-1500.

Age at death

The main criterion for approaching the age at death based on the hyoid bone in living human populations is the state of fusion of the greater horns with the body (O'Halloran and Lundy, 1987; Miller et al., 1998; Shimizu et al., 2005). However, there is a large degree of variation, and very late fusion or even nonfusion in elderly individuals is commonly encountered (O'Halloran and Lundy, 1987; Miller et al., 1998). Thus, it is not possible to estimate the age at death in the individuals represented by AT-1500 and AT-2000 based on the lack of fusion of the greater horns with the hyoid body.

At the same time, the ossification of the hyoid body begins very shortly after birth in living human populations (Reed, 1993) and progresses throughout infancy and adolescence as the dimensions of the hyoid body increase. The value for the maximum medial height approaches 10 mm (9.7 ± 2.4 mm) at around 15 years of age (Reed, 1993). The value in adult individuals in this same variable was found to be only slightly higher (11.7 ± 1.6 mm) in the present study. Importantly, the value for the maximum medial height in the adult Neandertal specimen Kebara 2 (13.4 mm) is 1.06 standard deviations (SD) above our adult modern human pooled-sex sample mean and 0.78 SD above our adult male mean (Table 2), suggesting that adult Neandertals reached similar values in the maximum medial height as do adult modern humans. This similarity in adult dimensions between modern humans and Kebara 2 suggests a late-adolescent or adult age status for both of the SH hyoid bodies, the maximum medial heights of which are easily encompassed within the adult modern human range of variation in the present study.

Table 2
Measurements (mm) and comparisons of the AT-1500 and AT-2000 hyoid bones

Specimen/sample	Maximum medial height	Maximum transverse diameter	Anteroposterior thickness	Depth of posterior surface	Thickness of the inferior border
Atapuerca AT-1500	10.8	21.8	6.8	2.8	1.7
Atapuerca AT-2000	10.2	18.6	6.7	1.6	1.3
Kebara 2	13.4 ¹	24.6 ¹	5.8 ¹	3.8 ¹	1.3 ²
SDR-034 ²	10.5	—	5.5	2.6	1.7
Modern humans (pooled sex; n = 60)					
Mean ± SD	11.7 ± 1.6	22.3 ± 2.7	8.6 ± 1.3	1.9 ± 0.7	
Range	7.9–15.7	16.6–30.6	5.4–11.1	0.6–3.9	
Modern human males (n = 45)					
Mean ± SD	12.3 ± 1.4	23.2 ± 2.2	8.9 ± 1.1	2.1 ± 0.7	
Range	8.9–15.7	18.6–30.6	6.9–11.1	0.6–3.9	
Modern human females (n = 15)					
Mean ± s.d.	10.1 ± 1.0	19.6 ± 2.3	7.8 ± 1.6	1.5 ± 0.5	
Range	7.9–11.5	16.6–24.2	5.4–11.0	0.9–2.6	

¹ Data are from Arensburg et al. (1989).

² Data are from Rodríguez et al. (2003).

Comparative morphological analysis

The anatomical descriptions of the SH hyoids clearly demonstrate that they are human-like in their morphology, and direct comparison between the SH specimens and the Neandertal specimens Kebara 2 and SDR-034 (Rodríguez et al., 2003) reveals some interesting details. All four specimens show a strong anterior tubercle. The fossae for the insertion of the geniohyoid muscles on either side of the midline are deeper and more defined in the Kebara 2 specimen than in AT-1500, and they are absent on AT-2000. The right and left lateral portions of the ventral surface, below the anterior tubercle, on Kebara 2 show fossae for the insertion of the omohyoid muscle (Arensburg et al., 1989). These are absent in AT-1500, while AT-2000 shows three smaller fossae inferiorly on either side of the midline for the attachment of the thyrohyoid, omohyoid, and sternohyoid muscles. At the same time, SDR-034 shows insertions for the geniohyoid, mylohyoid, hyoglossus, digastric, and stylohyoid muscles (Rodríguez et al., 2003). The dorsal aspect of AT-1500 shows a smooth concavity marked by a well-defined circular depression. This depression is absent in AT-2000 and the SDR-034 (Rodríguez et al., 2003) and Kebara 2 Neandertals, demonstrating some degree of variation in the expression of this trait in the fossil sample. Finally, the superior borders of AT-1500 and SDR-034 (Rodríguez et al., 2003) have a V-shaped contour, which is absent in AT-2000 and Kebara 2.

Thus, the single anatomical feature common to all the fossils is the presence of a marked anterior tubercle. In contrast, variation is present in the relief at muscular attachment sites, the morphology of the dorsal surface, and the contour of the superior border. These anatomical features also occur in modern human hyoid bodies (Fig. 2), although usually at low frequencies. In the small sample of 17 modern human hyoids, one specimen (5.9%) has a strong anterior tubercle (Fig. 2A),

another individual (5.9%) has a well-developed circular depression on the dorsal aspect (Fig. 2B), and two specimens (11.8%) have a V-shaped superior border (Fig. 2C, D). This last condition has also been reported to characterize 5.3% of a larger sample of modern human hyoid bones (Papadopoulos et al., 1989). Finally, there is also considerable variation in the degree of relief in the muscular insertion sites.

Metric analysis

The main metric dimensions in AT-1500 and AT-2000 are compared with Kebara 2, SDR-034, and a modern human sample in Table 2. The SH hyoids have very similar values in both the maximum medial height and the anteroposterior thickness, but AT-1500 has considerably larger values in the maximum transverse diameter and the depth of the posterior surface. Nevertheless, in all measurements, the values in the two SH hyoid bones fall well inside the range of variation of our modern human samples.

In comparison with Kebara 2, the SH hyoids have smaller values in the maximum medial height, maximum transverse diameter, and depth of the posterior surface. The SH fossils exceed Kebara 2 in the anteroposterior thickness but show similar values for the thickness of the inferior border. On the other hand, the values of maximum medial height and depth of the posterior surface in SDR-034 fall between those of the SH specimens. The SH hyoids have greater values than SDR-034 in the anteroposterior thickness and similar values in the thickness of the inferior border.

Figure 3 compares the maximum medial height and depth of the posterior surface (which describe the shape of the body in lateral view) in the SH hyoids, the two Neandertal specimens, and our modern human sample with the data provided by Alemseged et al. (2006) for *A. afarensis*, African apes, and modern humans. The two SH specimens, as well



Fig. 2. Anatomical variation in modern human hyoid bones. (A) Ventral view showing a well-developed anterior tubercle (Individual 1 from cadaveric collection). (B) Dorsal view showing a well-delimited round fossa (Individual 197 from San Pablo). (C) Superior view showing a V-shaped superior contour (Individual 64 from San Pablo). (D) Superior view showing a V-shaped superior contour (Individual 1 from cadaveric collection). Scale bar = 2 cm.

as the Neandertal hyoids, fall well inside the modern human distribution, and all of the *Homo* fossils are clearly different from *A. afarensis* and the African apes.

Sexual dimorphism

The range of variation among the SH fossils and the Neandertal specimens, in all the metric variables, is encompassed by that found to characterize living humans (Table 2), suggesting a degree of variation similar to that in *H. sapiens*. Sexual differences in hyoid-body dimensions have been identified in living populations, particularly in the maximum transverse diameter and the maximum medial height (Reed, 1993; Reesink et al., 1999; Kim et al., 2006; but see Miller et al., 1998), and the present study also found significant differences ($p < 0.001$) between the male and female mean values (Table 2) in these variables.

When these two variables are plotted against one another (Fig. 4), AT-2000 falls outside the male range of variation, suggesting a female attribution for this specimen, while AT-1500 falls in the region of overlap between the male and female distributions, making its sexual attribution unclear. Based on its associated pelvic anatomy, the Kebara 2 specimen has usually been considered male (Arensburg et al., 1985; Rak and Arensburg, 1987; Rosenberg, 1988; but see Tillier et al., 1989), and its hyoid dimensions clearly fall outside of the female range of variation (Fig. 3), suggesting a male attribution for this individual.

Discussion

The comparison between the SH, Neandertal, and modern human hyoids has revealed some interesting aspects.

Arensburg et al. (1989) reported that the depth of the posterior surface was the only measurement in the Kebara 2 Neandertal specimen that exceeded the range of variation of their modern human comparative samples. The present study has confirmed

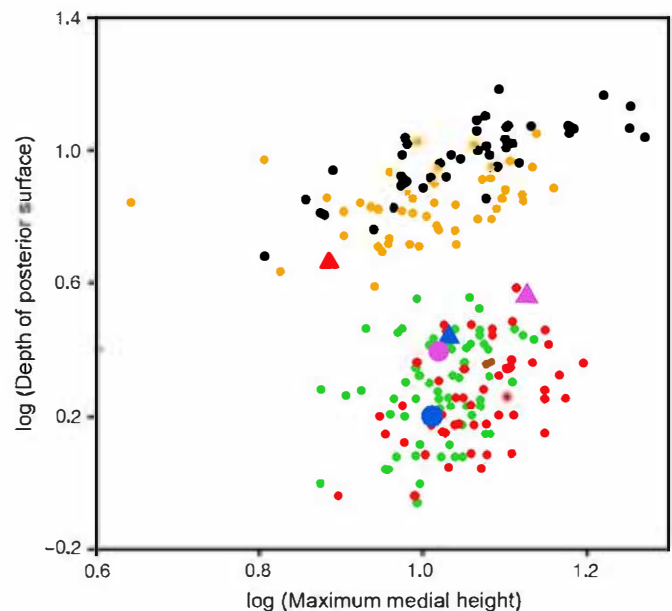


Fig. 3. Scatterplot comparing the values for logarithm of maximum medial height and logarithm of depth of posterior surface in the two SH specimens, Kebara 2, SDR-034, DIK-1-1, modern humans, chimpanzees, and gorillas. *Gorilla gorilla*, black circles; *Pan troglodytes*, orange circles; *Homo sapiens*, red and green circles; DIK-1-1, red triangle; AT-1500, blue triangle; AT-2000, blue circle; Kebara 2, magenta triangle; SDR-034, magenta circle. Data for *G. gorilla*, *P. troglodytes*, *H. sapiens* (green circles), and DIK-1-1 are from Alemseged et al. (2006). Data for Kebara 2 and SDR-034 are from Arensburg et al. (1989) and Rodríguez et al. (2003), respectively. Data for modern humans (red circles) are from present study. Adapted from Alemseged et al. (2006).

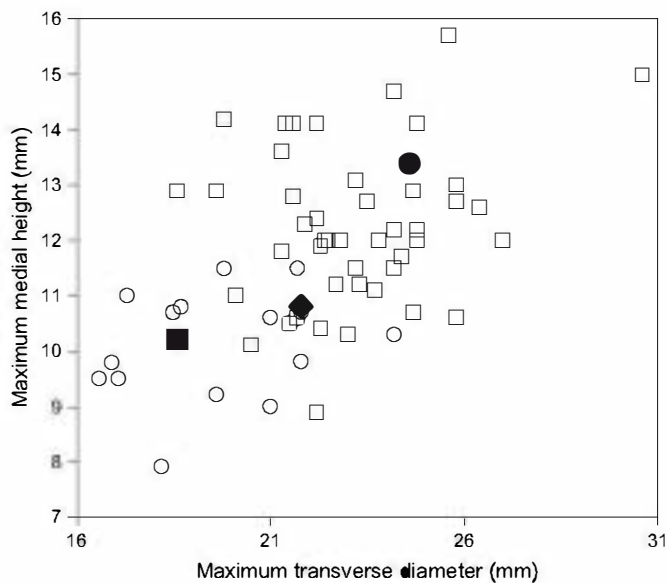


Fig. 4. Scatterplot comparing the values for the maximum transverse diameter and maximum medial height in the SH specimens, Kebara 2, and the pooled-sex modern human sample. Modern human males, open squares; modern human females, open circles; Kebara 2, solid circle; AT-1500, solid diamond; AT-2000, solid square. Data for Kebara 2 are from Arensburg et al. (1989).

this peculiarity in Kebara 2, whose depth of the posterior surface is greater than the other fossils and is almost 3 SD above the mean of our modern human sample, but is just within the upper limit of the range of variation. Nevertheless, the similarity in the values of the depth of the posterior surface in the SH specimens, SDR-034, and modern humans suggests that the condition in Kebara 2 is a particular feature of this specimen and should not be considered a Neandertal trait.

The anteroposterior thickness of the SH fossils is greater than that in both Neandertals, suggesting the possibility of a difference within the fossil sample. Nevertheless, these same differences exist between the modern human mean values in our sample (Table 2) and those of Arensburg et al. (1989) (5.13 ± 0.97 mm) and Rodríguez et al. (2003) (4.31 ± 1.06). Thus, the degree of variation found within the fossil sample is similar to that found in modern humans.

The thicknesses of the inferior borders of the SH and Neandertal specimens are very similar to one another and are well below the modern human mean (2.13 ± 0.42) provided by Rodríguez et al. (2003). Interestingly, this feature seems to be independent of the overall size of the hyoid body (Rodríguez et al., 2003), and it may represent a distinctive feature shared by the fossil specimens. Finally, all the fossils show a strong anterior tubercle, a feature that seems to occur at lower frequencies in modern humans, at least in our small comparative sample.

Despite these minor differences, it is clear that the SH hyoids, as well as both Neandertal specimens, exhibit a human-like morphology, clearly different from that found to characterize *A. afarensis* and the African apes. This finding suggests that modern human hyoid morphology is a very ancient feature of the genus *Homo*, one that was present in the last common ancestor of modern humans and Neandertals or perhaps even earlier.

Finally, we agree that the presence of a modern-human-like anatomy of the hyoid bone in a fossil specimen cannot be taken to demonstrate the existence of speech capacities (Lieberman et al., 1992). However, the presence in the SH fossils of a modern-human-like hyoid shows that some of the skeletal characteristics implicated in speech production in modern humans are very ancient features of the genus *Homo*. At the same time, the skeletal characteristics of the outer and middle ear associated with modern human auditory capacities and speech perception are also present in the SH hominins (Martínez et al., 2004).

Conclusions

The morphological and metric variation found in the SH and Neandertal specimens is of the same magnitude as that found to characterize living humans. Relying on modern human patterns and the evidence from the adult male Kebara 2 Neandertal hyoid, the SH fossils represent late adolescent or adult individuals, and AT-2000 is suggested to belong to a female individual. The SH fossils share with the Neandertals a high frequency of a strong anterior tubercle and a thin inferior border of the hyoid body, and they differ in the anteroposterior thickness of the body.

The hyoid bones recovered from the Sima de los Huesos represent the oldest fossil evidence for the anatomy of this bone in the genus *Homo*. Their morphology is modern-human-like and very different from that described for the African apes and *A. afarensis* (Alemseged et al., 2006). Thus, the genus *Homo* has been characterized by a modern-human-like anatomy of the hyoid bone since at least 530 ka. New discoveries of fossil hyoid bones will shed new light on the evolution of this bone in the human lineage and make it possible to contrast and refine the hypotheses presented here.

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