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James Steele

*University College London, j.steele@ucl.ac.uk*

Margaret Clegg

*Department of Palaeontology, Natural History Museum, London, m.clegg@nhm.ac.uk*

Sandra Martelli

*University College London*

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# Comparative morphology of the hominin and African ape hyoid bone, a possible marker of the evolution of speech

James Steele<sup>1\*</sup>, Margaret Clegg<sup>2</sup> and Sandra Martelli<sup>1</sup>

<sup>1</sup> AHRC Centre for the Evolution of Cultural Diversity, Institute of Archaeology, University College London, 31-34 Gordon Square, London WC1H 0PY.

<sup>2</sup> Department of Palaeontology, Natural History Museum, Cromwell Road, London, SW7 5BD. Email: [m.clegg@nhm.ac.uk](mailto:m.clegg@nhm.ac.uk)

\* Corresponding author. Email: [j.steele@ucl.ac.uk](mailto:j.steele@ucl.ac.uk)

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## Abstract

This study examines the morphology of the hyoid in three closely related species, *Homo sapiens*, *Pan troglodytes* and *Gorilla gorilla*. Differences and similarities between the hyoids of these species are characterised, and used to interpret the morphology and affinities of the Dikika *A. afarensis*, Kebara 2 Neanderthal, and other fossil hominin hyoid bones.

Humans and African apes are found to have distinct hyoid morphologies. In humans the maximum width across the distal tips of the articulated greater horns is usually slightly greater than the maximum length (distal greater horn tip to most anterior point of the hyoid body in the midline). A different pattern is usually found in the African ape hyoids, which have much greater maximum lengths. In humans, the hyoid body is also much more antero-posteriorly shallow in proportion to its height and width, and this is true for all age classes.

The Dikika australopithecine hyoid body proportions are chimpanzee-like. A discriminant function analysis, using a larger subadult sample from the three extant species than that reported by Alemseged *et al.* (2006), confirms this finding. The Kebara hyoid dimensions (body alone, and articulated body and greater horns) are almost all within the observed range for human hyoids. Discriminant functions clearly distinguish human from African ape hyoids, and classify the Kebara 2 hyoid as human (confirming the finding of Arensburg *et al.* 1989).

Our virtual dissection of a chimpanzee air sac system shows its subhyoid extension into the dorsal hyoid body. Following Alemseged *et al.* (2006), the expanded bulla characteristic of the African ape and australopithecine hyoid body is therefore interpreted as reflecting the presence of such a laryngeal air sac extension. Its absence in the human, Neanderthal, and *H. heidelbergensis* (Atapuerca SH) hyoids implicates the loss of the laryngeal air sacs as a derived Neanderthal and modern human trait, which evolved no later than the middle Pleistocene. If, as has been argued by de Boer, the loss of the air sac helped to enhance perceptual discrimination of speech sounds, then this derived hyoid morphology can be added to the list of fossil markers of the capacity for speech.

## **INTRODUCTION**

This study examines the morphology of the hyoid bone, its relationship with the air sac (where present), and its scaling with skull and mandible dimensions in three extant hominoid species, *Homo sapiens*, *Pan troglodytes* and *Gorilla gorilla*. Results from those tests are then used to inform interpretation of the *A. afarensis* hyoid from Dikika, Ethiopia (Alemseged *et al.* 2006), the Neanderthal hyoid from Kebara Cave, Israel (Arensburg *et al.* 1989), and other fossil hyoids from middle Pleistocene hominins, and to assess their implications for the evolution of hominin vocal tracts and the capacity for speech.

### *Hyoid anatomy in humans and great apes*

In adult primates, humans included, the hyoid presents approximately as a horseshoe shaped bone, located in the midsagittal plane of the neck, just inferior to the mandible and above the thyroid cartilage. The bones forming the adult primate hyoid are the unpaired body (basihyoid), the paired greater horns (thyrohyals) and the paired lesser horns (ceratohyals) (Liem *et al.* 2001; see also Senecail 1979). Developmentally, the hyoid bone is part of the pharynx, with the inferior half of the hyoid body and the greater horns originating from the third pharyngeal arch and the superior half of the hyoid body and the lesser horns arising from the second pharyngeal arch (Meikle 2002). The mammalian hyoid is usually suspended from the temporal bone via a series of small bone elements (such as the epihyal, stylohyal and tympanohyal, connecting to the lesser horns). However, in primates amongst some other mammalian groups, this series of bones is fused to the temporal bone in the form of a styloid process and the hyoid's lesser horns connect to it via the stylohyoid muscle and ligament (Liem *et al.* 2001). Further attachments of the hyoid are to the oral cavity floor by the suprahyoid musculature – especially geniohyoid and mylohyoid - and to the thyroid cartilage by the thyrohyoid membrane and the infrahyoid musculature. The hyoid forms the osseous base of the tongue and plays an important role in its motion. It also lifts the larynx, and thus plays a crucial role in swallowing (Dodds *et al.* 1990).

In humans, the hyoid body is flat and bar-shaped (see Figure 1). The greater horns have a tendency to fuse with the body after the age of 40 (bilaterally or unilaterally), but in many individuals, this is not the case even in old age (Miller *et al.*, 1998, O'Halloran and

Lundy, 1987). The human hyoid is positioned below the inferior margin of the mandibular body, approximately at the level of C3 to C4 and thus lies clearly below the tongue root.

In great apes on the other hand, the hyoid is placed superior to the inferior margin of the mandibular body and lies behind rather than below the tongue root (Falk 1975). Furthermore, the shape of the hyoid body differs both between the great apes and humans as well as between African and Asian great apes: African ape hyoid bodies are expanded anteriorly with a curved bulla, which reflects the superior extension of the laryngeal air sac into the hyoid body (e.g., Miller 1941; Aiello & Dean 1990). The African ape hyoid body can appear almost translucent due to the thinness of the bone. Although orangutans do not have an extensive hyoid body-bulla, they nevertheless have the most extensive and largest air sac system of all *Hominoidea* (Swindler and Wood 1973). The differences in hyoid body shape between the African and Asian great apes might be linked not to the presence or absence of the air sac system *per se* but to differences in how the subhyoid portion of the air sac reaches the pectoral and axillary regions in African and Asian great apes.

### *Laryngeal air sac anatomy*

Based on their origin as lateral outgrowths from the ventricular recesses formed by the inferior thyro-arytenoid fold and the vocal folds, the air sacs observed in all great apes are classified as lateral ventricular sacs (Hewitt et al., 2002, Kelemen, 1963, Negus, 1949, Avril 1963, Brandes 1932; Fick 1895; Miller 1941; Nemai and Kelemen 1929). However, in African great apes, the ventricular processes fuse to a single air sac space *within* the confinement of the hyoid body (see figure 2 for illustration) (Avril 1963 ; Miller 1941). It is this fused “stem” of the subhyoid portion of the air sac which emerges mid-sagittally through the thyrohyoid membrane of African great apes (Avril 1963; Miller 1941; Swindler and Wood 1973). It can therefore be argued that an air sac system with midsagittal plane exit point from the larynx complex forms a hyoid body bulla. That this might be the case is further supported by other primate species with air sac systems which differ from that of the *Hominoidea* (lateral ventricular sacs system) but which still leave the larynx complex via the thyrohyoid membrane in the midsagittal plane. Cercopithecoids (for example *Papio*) have subhyoid air sac systems which originate directly from the hyoid space rather than the laryngeal ventricles (Hewitt et al. 2002). However, they share the point of emergence of the

air sac with the African great apes (Avril 1963). In *Papio* and *Ateles*, there is bulla formation of the hyoid body observed (Hilloowala 1975, Swindler and Wood 1973).

Orang-utans contrast from this arrangement in that their ventricular processes pierce the thyrohyoid membrane *laterally*, below the greater horns of the hyoid (Fick 1895) rather than through the anterior aspect of the thyrohyoid membrane in the midsagittal plane. The two air sacs then fuse to a single sac below and anterior to the hyo-laryngeal complex. The orang-utan hyoid body on the other hand does not show an extensive, thin-walled bulla formation as seen in the African great apes, although some anterior swelling is observed in the supero-anterior wall of the orang-utan hyoid body (see e.g. Nemai and Kelemen 1929 for an image of an orang-utan hyoid body). The reason for the difference in these arrangements is not clear – perhaps it links to differences in suprahyoid musculature insertion on the hyoid between African apes and orang-utans. For example, the anterior belly of the digastric muscle is missing in orang-utans but present in African great apes (and humans) and the posterior digastric belly inserts into the angle of the mandible rather than the hyoid bone (Fick 1895; Nemai and Kelemen 1929; Swindler and Wood 1973). Perhaps this leads to a different arrangement in available space for the subhyoid air sac to emerge but further studies of air sac development would be necessary to test such a hypothesis.

With regards to the development of great ape air sacs there are only limited data available. Studies by Miller (1941) and Nishimura et al. (2007) suggest that the development of air sacs in African great apes occurs entirely postnatally. The very limited data available for the gorilla indicate that the hyoid air sac is already shaping a small hyoid cavity before the age of 2 years (Miller, 1941). A study of chimpanzee air sac development with MRI scans *in vivo* in three chimpanzees between age 1 month and 5 years (Nishimura et al. 2007) revealed an initial period of steady, relatively slow growth during early infancy up to 2 years of age. In this stage, the hyoid air sac continuously grows and is the most clearly visible part of the air sac system. In late infancy (age 2 to 5 years), a rapid descent and extension of the subhyoid part of the air sac system is observed. During this time, the air sacs reach the sternal level.

## *Laryngeal air sac function, and the loss of this system in human evolution*

If data on the anatomy of the great ape air sac are relatively scarce, it is even less clear what the function of primate laryngeal air sacs is (e.g. Hewitt et al. 2002; see also Kelemen, 1963, Negus, 1949, Nemai, 1926, Sonntag, 1924). In some primate species, air sacs, in junction with the vocal folds clearly play a role as a resonating chamber – especially in *Cercopithecoidea*, *Alouatta* (the howler monkey), and *Hylobates* (cf. Schon 1971, Schon Ybarra 1995; Hilloowala 1975). It has been suggested that air sacs can increase the duration and alter the formant frequencies of vocalization, perhaps as a means of exaggerating the body size of the caller (Fitch and Hauser 1995, Fitch 2000, de Boer 2009; Hewitt et al., 2002; cf. Hilloowala and Lass 1978). Riede et al. (2008) found - using a physical model - that air sacs can increase vocal variability (both by extending the dynamic range, and by increasing variability in vocal tract impedance). Nevertheless, both Riede et al. (2008) and de Boer (2009, 2012) also suggest that air sacs can introduce additional resonances into the vocal signal that would reduce the efficiency of a speech-like vocal communication system.

Of all the *Hominoidea*, only modern humans and some of the gibbon species do not have an air sac system and the possession of lateral ventricular air sacs is considered to be the ancestral state for the *Hominoidea* (Hewitt et al. 2002). This leads to further enquiries about the presence or absence of an air sac system in fossil hominoid taxa. The fossil record has yielded several complete or partial hyoids, of which the two best-known are one from the Kebara 2 Neanderthal (Arensburg et al. 1989) and one (represented by the body only) from the Dikika *Australopithecus afarensis* (Alemseged et al. 2006). These two bones represent very different moments in the evolution of the hominins, after the split of the last common ancestor of modern humans and African great apes. Additionally, in Spain the El Sidron site, dated to about 43 kya yielded a hyoid body assigned to Neanderthal which is very similar in size and shape to that of modern humans (Rodriguez et al. 2003), while the Sima de los Huesos site (also from Spain) has yielded two hyoid bodies, possibly belonging to a subadult and an adult specimen (Martinez et al. 2008), which are of great interest because they are attributed to middle Pleistocene European *Homo* (almost certainly ancestral to Neanderthals, and sometimes included in *Homo heidelbergensis*) and date to approximately 530 kya BP.

## *Aims of this paper*

The specific purpose of this paper is to describe the hyoid-air sac relationship in a chimpanzee, to provide a metrical analysis of hyoid characteristics in humans and in African apes that may relate to the presence or absence of a laryngeal air sac, and to characterize the fossil hyoids of extinct hominins in relation to those of these three living reference species. This paper revises and updates the data given in an unpublished analysis of hyoid metrical variation (Clegg 2001), and which have been used in two previous papers to contextualise and aid interpretation of individual fossil hominin hyoid bones (Alemseged et al. 2006; Martinez et al. 2008). In the wider research context, our work also relates to speech origins. Assuming both that the presence of air sacs can reduce the perceptual ease of discrimination of speech sounds, as argued by de Boer (2009, 2012), and that the common human and African great ape ancestor had an air sac system like that of the extant African great apes (expanding from the laryngeal complex via the thyrohyoid membrane in the midsagittal plane), then it can be argued that the loss of the air sac system in hominins is a marker of an enhanced capacity for articulate speech. It would therefore be of great interest to know at what point in time human ancestors lost the air sac system.



## **MATERIALS AND METHODS**

### *Chimpanzee air sac system: virtual dissection*

To study air sac morphology and hyoid relationships in a representative chimpanzee, a set of 3D Computer Tomography (CT) images of a chimpanzee cadaver was recorded in December 2007 at the Hospital Balgrist, Zurich, using a specimen from the A.H. Schultz and Primate Collections of the Anthropological Institute and Museum of the University of Zurich, Switzerland. The chimpanzee specimen (catalogue number 7288, Zurich Collections) used for the surface reconstruction of the air sac system was a juvenile male. Age is estimated at 4 to 5 years of age. The specimen originally came from the Department of Anatomy, University of Zurich and has been with the anthropology cadaver collections since 1966. The animal was a wet preserved cadaver; conservation is maintained with formaldehyde solution (4%). We used CT scan technology (Philips Brilliance 40 Medical Systems, slice thickness 0.67 mm, Inc. 0.33 mm, tube voltage 120 kV, tube current base line 120 mA, FOV 160 mm, all image matrices 512 x 512 x 512). From the CT scans, the volume of the air sac system was segmented from their entrances in the laryngeal ventricles and reaching both supra- and infra-laryngeal extensions using the software AMIRA® (Visage Imaging™). Segmenting means that the pixels of each slice image are assigned a label describing to which region or material the pixel belongs. A new data set is then created and a surface grid is produced from it which allows for making a 3D view of the selected object's surface. All visualizations (slices, volume surface reconstructions) were produced with AMIRA 4.1.1.

### *African ape and human hyoid morphology: osteological study*

African ape skeletal elements were from the Merfield and Congo expedition collections held by the Powell-Cotton Museum, Kent, England, and adult human skeletal elements were from the Christ Church Spitalfields collection held by the Natural History Museum, London, England. Hyoid bones were recorded for 118 adult individuals — 64 humans *Homo sapiens* (38 males, 23 females, 3 unsexed), 33 chimpanzees *Pan troglodytes* (7 males, 26 females), and 21 gorillas *Gorilla gorilla* (10 males, 11 females) —

with additional measurements of the associated cranium and mandible when present. All species were assessed as adult on the basis of third molar in occlusion or, if the third molar was missing or impacted, tooth wear pattern on M1 and M2. The measurements taken are described in Table 1. Hyoid body measurements were also taken for a smaller number of infants and juveniles in the same collections (2 *Homo sapiens*, 17 *Pan troglodytes*, 21 *Gorilla gorilla*), and for an additional human sample of 27 infants, juveniles and adolescents from the Mediaeval skeletal assemblage from Wharram Percy, Yorkshire, England. Figure 1 illustrates examples of adult human, chimpanzee and Neanderthal hyoid bones.

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FIGURE 1 ABOUT HERE

TABLE 1 ABOUT HERE

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The hyoid bone measurements were based on those that Arensburg and colleagues used to analyse the Kebara 2 Neanderthal hyoid bone and human comparisons (Arensburg *et al.*, 1989, 1990), with an additional new measurement that captures the variation found when comparing human and African ape hyoids. The African ape hyoid bodies are often expanded anteriorly with a curved bulla, which may reflect the superior extension against the dorsal hyoid body of the laryngeal air sac (e.g., Aiello & Dean 1990). Arensburg *et al.* (1989)'s antero-posterior thickness measurement (APT) is compromised as a thickness measurement in the African ape bones by the fact that the upper and the lower posterior margins of the hyoid body are not equivalent in their posterior extension, since the upper margin typically extends a greater distance posteriorly in these species. The new measurement MAPT controls for this shape characteristic.

The dimensions of the Dikika hyoid were taken from Alemseged *et al.* (2006), whose comparative analysis of its form used an unpublished earlier version of the chimpanzee and gorilla data reported here, with some additional cases (F. Spoor, pers. comm.). All metrical data reported in the present paper were collected by MC and JS during 2006 and 2007 (new or re-measured), and supersede the values reported in an earlier iteration (Clegg 2001) and which were used by Alemseged *et al.* (2006) and by Martinez *et al.* (2008). The comparative sample used by Alemseged *et al.* (2006) also included only three human subadults (two from Christ Church, Spitalfields, and one other). For the present study, we expanded the human subadult sample to 29 individuals, so that our analysis of Dikika in the

present paper could make comparisons with a more appropriately age-matched sample from all three extant species. In these respects, the present comparative analysis of the morphology of the Dikika hyoid body should be seen as complementing that of Alemseged *et al.* (2006). The dimensions of the Kebara 2 hyoid were taken from Arensburg *et al.* (1989), except MAPT which was taken from a high-quality cast.

### *Statistical analysis*

Descriptive statistics were obtained for all adult hyoid dimensions measured in the three extant species, and discrimination function analysis of these three groups was used to classify extant specimens from each of two extinct species, *Australopithecus afarensis* and *Homo neanderthalensis*. The scaling of dimensions was estimated by reduced major axis regression (Sawada 1999), and the test for isometry was whether or not a value of 1.0 fell within the 95% confidence interval for the slope of the log-log regression.

Predicted morphological relationships of the hyoid with the craniofacial and laryngeal complexes include those between the total maximum breadth of the hyoid (distance between the distal greater horns in their anatomical positions) and transverse diameter of the basal oropharynx, and between total maximum length of the hyoid and mid-sagittal diameter of the basal oropharynx and tongue root. Soft tissue dimensions were not available to test these predictions in our samples. To explore these relationships indirectly, a set of cranial dimensions was measured in the adult human and African ape sample (Table 2), and bivariate correlations calculated to estimate the covariance of each hyoid dimension with the most highly correlated cranial variable in the three extant species. The expectation was that hyoid widths would scale most closely with one or more width measurement on the cranial base or facial skeleton, and that hyoid lengths would scale most closely with one or more cranial base length measurement.

Statistical analyses were undertaken using SPSS for Windows, version 14.0 (SPSS Inc., 2005), and the reduced major axis regression add-in for Microsoft Excel (Sawada 1999).

## **RESULTS**

Our results support a clear distinction between the African ape and human hyoid body morphologies, which (as our virtual dissection confirms) relate to underlying contrasts in the presence or absence of the infrahyoid extension of the air sac system. Multivariate analyses support the reconstruction of a chimpanzee-like air sac system in earlier hominins (*A. afarensis*), and of the absence of this system in later hominins (*H. heidelbergensis*, *H. neanderthalensis*). Overall dimensions of the hyoid (body plus greater horns) are associated across species with width and length variation in the cranial base.

### *The chimpanzee air sac system.*

Our virtual dissection study yielded a clear illustration of the relationship between the laryngeal air sac and the hyoid body in an African ape. Figure 2 shows an image of the head and neck of the male subadult chimpanzee, consisting of a midsagittal plane slice combined with a coronal section. The expansions of the hyoid air sac and the midline process (labelling of air sacs as defined by Miller, 1941) are clearly visible. Some other clearly identifiable anatomical structures are labelled as well. Figure 3 shows a superimposition of the surface reconstruction of the air sac system combined with a midsagittal plane slice. In Figure 3, only features of the air sac system lying anterior to the midsagittal plane slice are visible. However, clearly visible are the greater horn of the hyoid as well as the submaxillary air sac, the infrahyoid air sac (midline passage), infraclavicular air sac and the episternal air sac. Since this is a juvenile animal, the episternal air sac did not reach further down than approximately halfway to the manubrium. Figure 4 shows another view of a combination of the surface reconstruction of the air sac system and in this case a coronal section (approximately at the level of the sphenomaxillary border, behind the sphenoid sinus. The anterior third of the temporal bone, but behind the maxilla and mandible is visible). This image has been chosen because it shows where and how the air sac system branches off the pharynx and trachea.

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FIGURE 2 ABOUT HERE

FIGURE 3 ABOUT HERE

FIGURE 4 ABOUT HERE

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FIGURE 5 ABOUT HERE

FIGURE 6 ABOUT HERE

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Additional interesting details are visible in the image of the surface reconstruction of the hyoid bone and air sac system only – as shown in Figure 5. Although the view on the hyoid air sac is obscured by the hyoid bone, relationships between the different air sacs show quite well. Ventricular and thyrohyoid processes are visible too although the exact connection to the air sacs is somewhat unclear in this image. To further visualize the connections between the pharynx, trachea and the processes of to the air sac system, the final image (Figure 6) is presented. The air sac system is shown from posterior and the surfaces are rendered semi-transparent for better visualization of overlaying structures. The image first shows that the left side is the dominant part of the air sac system of this specimen. The image also reveals that not only do the ventricular processes lead to the left and right sides of the air sac system but that there is a connection, located anteriorly and in the midline between the air sac system and the trachea. The air sac system becomes asymmetric just after the processes leading to the submaxillary air sacs are branching off: The left thyrohyoid process clearly connects to the hyoid air sac and the left midline process then leads to left and right pectoral air sacs, episternal air sac and left and right infraclavicular air sacs. The right thyrohyoid process on the other hand ends blind without connecting to the hyoid air sac.

*Adult human and African ape hyoids.*

The mean and range of values for metrical attributes of adult hyoids for each species are shown in Table 2. Three distinct patterns emerge. First, adult African ape hyoids have an anteroposteriorly expanded body compared to the human hyoids, with the presence of a posterior cavity or bulla reflected in the large differences between humans and the African apes in depth of the posterior surface of the body (DPS) and its maximum antero-posterior thickness (MAPT). This contrast is not found in other adult hyoid body dimensions (body height, MMH, or body width, MTD). Secondly, in humans the maximum width across the distal tips of the articulated greater horns (TMB) is usually slightly greater than the maximum length (TML, distal greater horn tip to most anterior point of the hyoid body in the

midline). A different pattern is found in the African ape hyoids, which have much greater maximum lengths. Thirdly, within the African apes the mean anteroposterior dimensions of the adult gorilla hyoid bodies are greater than those of the adult chimpanzee hyoid bodies, although the bones of these two species are not statistically distinguishable in the other two dimensions (maximum transverse diameter, MTD, and maximum medial height, MMH). These contrasts are confirmed by the *t*-tests of differences between means for each possible pairing of species (Table 3).

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TABLE 2 ABOUT HERE

TABLE 3 ABOUT HERE

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In the discriminant function analysis some of the hyoid measurements were excluded. TML and TMB were excluded because the sample of articulated bodies and greater horns in *Gorilla* was too small to make the analysis meaningful with these measurements included. APT was excluded to prevent redundancy, given the inclusion of the new alternative measurement MAPT.

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TABLE 4 ABOUT HERE

TABLE 5 ABOUT HERE

FIGURE 8 ABOUT HERE

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The first discriminant function analysis included measurements from both the hyoid body and the (disarticulated) greater horns. The coefficients and the structure matrix (Tables 4a, 4b) indicate that DF1, which accounts for 96% of the variance (Wilks'  $\lambda = 0.032$ ,  $p < 0.001$ ), reflects primarily variation in the anteroposterior depth of the body. MAPT and DPS have the highest correlations on this factor. This analysis shows a clear division between humans and the African apes (Fig. 8a). Human hyoids have a shallow body compared with the African ape species. DF2 accounts for only 4% of the variance (Wilks'  $\lambda = 0.583$ ,  $p < 0.001$ ), and is therefore not considered further. All the humans and

chimpanzees and all but one of the gorillas were correctly classified by this analysis (Table 4c).

The second discriminant function analysis included measurements from the hyoid body only, enabling a larger sample to be used (Figure 8b). The coefficients and the structure matrix (Tables 5a, 5b) indicate that DF1, which accounts for 99.3% of the variance (Wilks'  $\lambda = 0.05$ ,  $p < 0.001$ ), also reflects variation in the anteroposterior depth of the body. MAPT and DPS, which diagnose hyoid body thickness differences between humans and African apes, again have the highest correlations on this factor, confirming the first analysis. Classification results were also similar, although the inclusion of a larger number of individuals resulted in three chimpanzee hyoids being misclassified as gorilla, and three gorilla hyoids being misclassified as chimpanzee (Table 5c).

#### *Kebara adult Neanderthal hyoid.*

The measurements of the adult Kebara 2 hyoid fall within the observed range for adult human hyoids in almost all dimensions (Table 2). The exception is MAPT, for which the Kebara value of 8.0 mm is marginally higher than the observed range for the human sample (3.4-7.6 mm). This higher value for MAPT reflects the relatively pronounced medial crest for attachment of the geniohyoid muscle, which Arensburg *et al.* (1989) suggested would have been unusually robust given the large size of the associated Kebara 2 mandible. Compared with the African apes, the Kebara hyoid is smaller than the observed range for total length (TML) and for length of the greater horn (LGH), is wider between the distal tips of the articulated greater horns (TMB), and is shallower in body depth (DPS, MAPT). This is consistent with the human pattern. The Kebara hyoid falls within the observed range for all three species for other, less differentiating, dimensions (MTD, MMH, WGH). The discriminant functions classify the Kebara hyoid as human in both cases (based on body and horns, and on body only; see Tables 4c and 5c).

#### *Subadult human and African ape hyoids.*

The contrasts found in the adult hyoids are also found in the subadults. Compared with humans, the subadult African ape hyoids have an anteroposteriorly expanded body

with the presence of a posterior cavity or bulla, as can be seen in plots of the depth of the posterior surface (DPS) against both width (MTD) and height (MMH) (see Figure 9a). The ontogenetic scaling trends are summarised in Table 6, and indicate that at all ages, the human values for DPS are very significantly lower than those of either African ape for any given value of MTD or MMH, as indicated by the different values for the intercept in the regression models. In African apes the depth of the bulla (DPS) is greater from an early age, and also hyperscales to the hyoid body's other linear dimensions (width, MTD and height, MMH), reflecting the growth of the air sac system. Width (MTD) and height (MMH) of the hyoid body scale isometrically in chimpanzees but MMH hyperscales relative to MTD in gorillas, reflecting an additional dimension of expansion of the gorilla hyoid bulla (the air sac growth presumably causing the hyoid bulla to expand superiorly as well as anteriorly, relative to its transverse diameter).

A discriminant function analysis of the subadult sample based on the three hyoid dimensions reported for the Dikika specimen (Alemseged *et al.* 2006) correctly classifies all the humans, and the majority of the chimpanzees and gorillas (a small minority of each ape species being misclassified as the other; see Table 7). The first discriminant function is the only statistically significant one (Wilks'  $\lambda = 0.129$ ,  $p < 0.001$ ), and DPS has the strongest loading on it. A high value for DF1 indicates a relatively deep posterior surface in proportion to the height of the hyoid body.

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TABLE 6 ABOUT HERE

TABLE 7 ABOUT HERE

FIGURE 9 ABOUT HERE

FIGURE 10 ABOUT HERE

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#### *Dikika juvenile hyoid dimensions.*

As previously observed by Alemseged *et al.* (2006), and now confirmed with a larger subadult human sample and with only subadults considered, the Dikika juvenile australopith hyoid is deep for its height and width (Figure 9), and is morphologically chimpanzee-like. This similarity applies both when comparing only subadults from the three extant species



(Figure 9a), and when comparing across all observed age classes (Figure 9b; this graph also shows the plotted values for the two middle Pleistocene European hominin hyoids from Atapuerca SH, attributed here to *H. heidelbergensis*). The discriminant function analysis of subadult hyoid bodies, based solely on the three hyoid body dimensions reported for the Dikika specimen, also classifies this specimen with chimpanzees (Table 7; Figure 10).

### *Adult cranial and hyoid shape*

Bivariate correlations between hyoid and cranial dimensions (Table 8) indicate that in the adults (with all three extant species pooled), hyoid total maximum length, greater horn length, and body thickness are all most highly correlated with cranial base length (orale-endobasion; vs. TML, Pearson's  $r = 0.92^{**}$ ; vs. LGH, Pearson's  $r = 0.75^{**}$ ; vs. DPS, Pearson's  $r = 0.92^{**}$ ; vs. MAPT, Pearson's  $r = 0.95^{**}$ ). The scatterplot of MAPT vs. O-E (Figure 11) suggests that this correlation may simply reflect a size effect in both dimensions that differentiates mean values in the three species. When the sample is split into the three extant species, this pattern of statistically significant correlation only holds for the gorillas. However, there may be some overall functional significance in the fact that anteroposterior thickness of the hyoid body correlates with a cranial base dimension taken in the same plane.

Total maximum breadth of the hyoid is most highly correlated with bicarotid canal width (TMB vs. CC-CC, Pearson's  $r = 0.71^{**}$ , all three species pooled). When broken down by species, this correlation is also supported by the chimpanzee data, and in humans, the highest correlation is with the closely-related dimension of bistylomastoid width (TMB vs. SM-SM, Pearson's  $r = 0.50^*$ ); the gorilla sample is too small for independent assessment. This result is consistent with the soft tissue relationships: the styloid process is connected to the hyoid via the stylohyoid ligament and muscle, while the carotid artery passes just lateral to the superior thyroid cartilage and bifurcates at the level of the C3 vertebra, the internal branch passing more medially to enter the skull via the carotid canal. Bistylomastoid foramen and bicarotid canal width might therefore be expected to scale with the transverse diameter of the larynx and pharynx.

The width of the hyoid body correlates most highly with bicondylar breadth of the mandible (MTD vs. MBB, Pearson's  $r = 0.59^{**}$ , all three species pooled; Figure 12a), and is next-most highly correlated with mandibular bigonial breadth (MTD vs. MGB, Pearson's  $r =$

0.55\*\*, all three species pooled), which must also reflect a size relationship between these closely contiguous structures. In the Kebara Neanderthal, the scaling of maximum bigonial breadth of the mandible to maximum transverse diameter of the hyoid body is consistent with this observed relationship in the extant species (Figure 12b).

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TABLE 8 ABOUT HERE

FIGURE 11 ABOUT HERE

FIGURE 12 ABOUT HERE

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## **DISCUSSION**

Humans and African apes form a distinct clade, within which it is relevant to look for phenotypic evidence of divergent behavioural evolution. Human and African ape hyoid bones have distinct morphologies. The hyoid measurements recorded in this study from a human sample from early modern London reproduce with remarkable consistency the pattern found by Arensburg *et al.* (1989), in their earlier study of five Holocene human populations from Europe and the Near East (see Table 9). Human hyoids usually have a slightly greater total maximum breadth than total maximum length, and their bodies are relatively shallow anteroposteriorly, although their maximum transverse diameters do not differentiate them from the African apes.

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TABLE 9 ABOUT HERE

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The discriminant function coefficients indicate that the hyoids of the African apes and of humans are principally distinguished by the relative depth of the body (i.e. the presence or absence of the expanded bulla), which reflects the presence or absence of a subhyoid airsac extension (as our chimpanzee virtual dissection clearly illustrates). The discriminant function analysis did not misclassify any adult human hyoids. The adult chimpanzee and gorilla hyoids are more similar, to the extent that a small minority of examples from one species were wrongly classified as the other, in the post hoc analysis. The primary difference in the African ape bones is in their total maximum length and in the depth of the body, the gorilla hyoids being on average larger in these dimensions than the chimpanzee examples even after controlling for hyoid body width and height.

We predicted that total maximum length (TML) of the hyoid would covary with antero-posterior length of the basal oropharynx and tongue root, and that total maximum breadth (TMB) of the hyoid (distance between the distal greater horns in their anatomical positions) would covary with transverse diameter of the basal oropharynx. Published soft tissue measurements of adult humans are consistent with these expectations. Perrier *et al.* (1992) found the transverse diameter of the basal oropharynx to be 41 mm in a cast from a single adult vocal tract, which is in the middle of the range for TMB in our own adult skeletal sample ( $40.7 \pm 5.2$  mm.,  $n=21$ ). The pharyngeal cavity at this level is longer in transverse

than in sagittal diameter, and it is the sagittal diameter of the tongue root which makes the additional contribution to TML. Taylor *et al.* (1996) found the average distance from the superior point of the anterior hyoid body to the posterior wall of the pharynx in the midline to be 28 mm in females and 35 mm in males, based on samples of 18 year-olds measured from lateral cephalometric radiographs. This is approximately consistent with our own findings of an overall mean adult TML of 36 mm, with a mean for adult females (n=17) of 34 mm, and a mean for adult males (n=20) of 38 mm. It would be useful in future to collect more data on oral and pharyngeal cavity dimensions in chimpanzees and gorillas, so that species differences in hyoid dimensions can also be correlated more precisely with the dimensions of these soft tissue structures and the relevance inferred for any functional differences in (e.g.) swallowing movements. In the African apes, the relatively large values found for TML also reflect a third factor — the greater depth and curvature of the hyoid body itself, which is filled by a laryngeal air sac.

Examining the fossil hyoids and comparing them with the modern hominoid samples show that the Dikika *A. afarensis* hyoid has the expanded bulla found in the African apes associated with retention of the laryngeal air sac with its subhyoid extension (Alemseged *et al.* 2006).

The Kebara Neanderthal specimen and the hyoid body of the juvenile *Australopithecus afarensis* from Dikika, Ethiopia (Alemseged *et al.* 2006) are not the only published hyoids from extinct hominins, although they are the best-known. Hyoids of extinct hominins were also found at two Spanish sites. In Spain the El Sidron site, dated to about 43 kya yielded a hyoid body assigned to Neanderthal which is very similar in size and shape to that of modern humans (Rodriguez *et al.* 2003). The Sima de los Huesos site (also from Spain) yielded two hyoid bodies, possibly belonging to a subadult and an adult specimen (Martinez *et al.* 2008). These two hyoids are of great interest because they are attributed to pre-Neanderthal archaic *Homo* (*Homo heidelbergensis*) and date to approximately 530 kya BP. The absence of an expanded bulla in these hyoid bodies of humans, Neanderthals and *Homo heidelbergensis* suggests that they shared the derived feature of an absence of laryngeal air sacs. There is no evidence, nor to our knowledge any plausible functional reason to expect, that later hominins passed through an orangutan-like stage with a large air sac that did not impinge on the hyoid body. Such a suggestion would lack parsimony. The loss of the air sac system can therefore be dated to no later than the middle Pleistocene.

Our study has focused on comparative hyoid bone morphology in African apes and humans, and its implications for the presence or absence of an air sac system. If the presence of an air-sac system hinders the production of easily-perceptible contrasts in basic speech sounds and its absence in humans reflects selection against that hindrance (as de Boer has proposed based on his experimental and modelling work; de Boer 2009, 2012), then the emergence of human-like speech can also therefore be dated to no later than the middle Pleistocene. Our comparative analysis was, by its nature as a dry bone study, unable to identify any association between the shape or size of the hyoid bone and its position in relation to the mandible; our study therefore sheds no new light on the vexed question of the lengths of the vertical and horizontal portions of the supralaryngeal vocal tract in fossil hominins (cf. Fitch 2009). However, elsewhere we have explored the reconstruction of the Neanderthal vocal tract using three-dimensional shape analyses and software articulatory models of vowel production, with hyoid position predicted by extrapolation from a reference sample of head-and-neck scans of adult humans (Barney et al. 2012); similarly to Boe et al. (2002, 2011), we found that the reconstructed Neanderthal tract has comparable properties to those of humans, although the necessity of estimating fossil hominin soft tissue relationships from an extant reference species limits independent validation of the modelling assumptions. The presence in Neanderthals of the human variant of the FOXP2 gene (Krause et al. 2008, Burbano et al. 2010), the possible skeletal evidence of adaptations for ‘speech breathing’ (Maclarnon and Hewitt 1999, 2004), the skeletal evidence for *H. heidelbergensis* and Neanderthal right-handedness (e.g. Steele and Uomini 2009, Frayer et al. 2012, Volpato et al. 2012) and the presence in Neanderthals of the human pattern of cerebral petalias (e.g. Barzeau et al. 2012), provide additional independent supporting evidence for a capacity for speech in these fossil hominins.

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**Table 1.** Hyoid and cranial measurements. Unilateral measurements taken on left side where available.

Measurement		Description
<b>Hyoid bone measurement (after Arensburg et al. 1989, 1990; except MAPT, defined for this study)</b>		
TML	Total maximum length	Total maximum length of the hyoid bone in the mid-sagittal plane, in projection from the distal end of the greater horns to the most antero-medial point of the body, with the greater horns attached to the body in their anatomical position.
TMB	Total maximum breadth	Total maximum breadth of the hyoid bone in transverse plane, taken at the most external distal ends of the greater horns, with the greater horns attached to the body in their anatomical position
MTD	Maximum transverse diameter	Maximum transverse diameter of hyoid body
MMH	Maximum medial height	Maximum medial height of hyoid body (midsagittal distance between the supero-posterior and infero-posterior borders of the hyoid body)
APT	Antero-posterior thickness	Antero-posterior thickness of hyoid body in sagittal plane; one caliper branch tangent to upper and to lower posterior margins of hyoid body, the other branch tangent to the most protruding antero-medial point of the hyoid body
MAPT	Maximum antero-posterior thickness	Chord length in sagittal plane, from medial point on upper posterior margin of hyoid body, to the most protruding antero-medial point of the hyoid body
DPS	Depth of the posterior surface	Depth of the posterior surface of the hyoid body, measured from the the upper and the lower posterior margins of the hyoid body in the mid-sagittal plane
LGH	Length of the greater horn	Distal end to the lateral border of proximal articular surface
WGH	Width of the greater horn	Infero-superior width of greater horn taken at widest point closest to hyoid body
<b>Skull measurements</b>		
U.FACE	Upper facial height	From nasion to alveolare
BIZYGO	Bizygomatic breadth	From zygion to zygion
IPL	Internal palate length	From orale to staphylion
IPB	Internal palate breadth	From endomolare to endomolare
MBB	Mandibular bicondylar breadth	From condylion to condylion
MGB	Mandibular bigonial breadth	From gonion to gonion
S. HT	Mandibular symphysis height	From gnathion to infradentale
ML	Mandibular length	Horizontal distance from the posterior aspect of condyles to gnathion
HR	Maximum height of mandibular ramus	From gonion to uppermost part of condyle
C-E	Cranial base length	Hormion to endobasion
O-E	Total cranial base length	Orale to endobasion
TP-TP	Bitympanic width	Cranial base width at most inferior point of lateral end of tympanic plates
SM-SM	Bistylomastoid width	Width between central points in the left and right stylomastoid foramina
CC-CC	Bicarotid canal width	Width between central points in the left and right carotid canals
TP-PA	Tympanic-petrous length	Length between most inferior point of lateral end of tympanic plate and anteriormost point of inferior surfaces of petrous temporal bone

**Table 2.** Descriptive statistics for adult human, chimpanzee, and gorilla hyoid bones, with individual values for Neanderthal (Kebara 2) and *A. afarensis* (Dikika). Measurements in millimetres.

		<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>
<b>TML</b>	Mean, SD	36±4.1	48.3±4.5	67.3±1.1
	n, range	n=37; 27.8-42.4	n=5; 43.3-55	n=2; 66.5-68
<b>TMB</b>	Mean, SD	40.7±5.2	31.2±5.4	32.8±5.9
	n, range	n=21; 30.7-50.6	n=5; 24.1-37.4	n=2; 28.6-37
<b>MTD</b>	Mean, SD	23.4±2.5	23.5±2.6	25±3.6
	n, range	n=62; 17.1-29.9	n=31; 17.7-29	n=18; 18.8-31.5
<b>MMH</b>	Mean, SD	10.6±1.2	11.1±1.7	13.1±3.3
	n, range	n=63; 8-13.7	n=32; 8-14.4	n=18; 7.5-18.2
<b>APT</b>	Mean, SD	5.1±1	7.3±1.3	11.6±3
	n, range	n=63; 3.1-7.4	n=31; 5.4-10.4	n=17; 6.2-17.5
<b>MAPT</b>	Mean, SD	5.1±1	13.4±1.9	17.1±2.9
	n, range	n=63; 3.4-7.6	n=31; 8.7-16.8	n=17; 11.5-21.4
<b>DPS</b>	Mean, SD	2±0.7	6.6±1.4	9.9±2.4
	n, range	n=63; 0.9-3.8	n=31; 3.9-10	n=17; 5.7-14.6
<b>LGH</b>	Mean, SD	28.1±3.8	33.6±5.4	40±7.6
	n, range	n=41; 19.2-35.5	n=27; 26-51.6	n=15; 30.5-51.8
<b>WGH</b>	Mean, SD	7±1.1	7±1.3	9.5±2.1
	n, range	n=49; 5.2-9.3	n=28; 4-11.7	n=17; 6-13

**Table 2 (continued).** Descriptive statistics for adult human, chimpanzee, and gorilla hyoid bones, with individual values for Neanderthal (Kebara 2) and *A. afarensis* (Dikika). Measurements in millimetres.

	<b>TML</b>	<b>TMB</b>	<b>MTD</b>	<b>MMH</b>	<b>APT</b>	<b>MAPT</b>	<b>DPS</b>	<b>LGH</b>	<b>WGH</b>
<b>Dikika<sup>1</sup></b>	-	-	11.7	7.7	-	-	4.7	-	-
<b>Atapuerca AT-1500<sup>2</sup></b>	-	-	21.8	10.8	6.8	-	2.8	-	-
<b>Atapuerca AT-2000<sup>2</sup></b>	-	-	18.6	10.2	6.7	-	1.6	-	-
<b>SDR-034<sup>3</sup></b>	-	-	-	10.5	5.5	-	2.6	-	-
<b>Kebara<sup>4</sup></b>	35.5	45.0	24.6	13.4	5.8	8.0	3.8	25.0	5.2

<sup>1</sup> Juvenile *Australopithecus afarensis*. From Alemseged *et al.* (2006), online supplementary material

<sup>2</sup> *Homo heidelbergensis*. From Martinez *et al.* (2008).

<sup>3</sup> Neanderthal. From Rodriguez *et al.* (2003).

<sup>4</sup> Neanderthal. From Arensburg *et al.* (1989), except MAPT, taken from a cast

**Table 3.** T-tests for comparison of means for adult hyoid bone measurements (estimated with or without equality of variance assumed, according to results of Levene's test for each paired comparison)

	<i>HomolPan</i>	<i>HomolGorilla</i>	<i>Pan/Gorilla</i>
TML	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.003</b>
TMB	<b>0.001</b>	0.056	0.744
MTD	0.872	0.094	0.094
MMH	0.229	<b>0.006</b>	<b>0.02</b>
APT	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
MAPT	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
DPS	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
LGH	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.008</b>
WGH	0.983	<b>&lt;0.001</b>	<b>&lt;0.001</b>

Significance levels:  $\alpha=0.002$  for  $p<0.05$  after applying Bonferroni's correction for multiple comparisons (n=27 tests).