A Reanalysis of Anatomical Changes for Language: Re-Dating the Loss of Laryngeal Air Sacs in *Homo sapiens*

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Abstract

Laryngeal air sacs occur in many different species of primates. In the case of Homo sapiens, their presence has been lost. This has been argued to have occurred before Homo heidelbergensis, due to a loss of the bulla in the hyoid bone from Australopithecus afarensis (Martinez, 2008), at a range of 500kya to 3.3mya. (de Boer, to appear). Justifications for the loss of laryngeal air sacs include infection, the ability to modify breathing patterns and the reduction of a need for an antihyperventilating device (Hewitt et al. 2002), and linguistic selection against air sacs as they are disadvantageous for subtle, timed, and distinct sounds, (de Boer, to appear), Further, it has been suggested that the loss goes against the significant correlation of air sac retention to evolutionary growth in body mass (Hewitt et al., 2002). I argue that the loss of air sacs may have occurred more recently than 3.3mya, as the loss of the bulla in the hyoid does not exclude the possibility of airs sacs, as laryngeal air sacs can herniate between two muscles regularly in other species (Frey et al., 2007), and as vestigial air sacs in Homo sapiens indicate a shorter evolutionary timescale. Further, I argue that Homo sapiens was not an exception to the smaller body weight and loss correlation, as a size reduction in Homo sapiens from Homo heidelbergensis was not accounted for in the previous synchronic study. It is hoped that these arguments will shed light on the anatomical pre-adaptations or adaptations for language use in hominins.

1 Introduction

Air sacs are found in a wide variety of different animals; in mammals, they appear in bats, cetaceans, and ungulates, among other orders (Bradbury 1998). Laryngeal air sacs, which are connected to the vocal tract and situated above the vocal folds, appear in many primates – including all of the apes, excluding *Homo sapiens*. Many studies, citing Avril (1963), associate the bulla, an extension of the hyoid bone, as being incontrovertibly linked with the presence of air sacs in the ape lineage. From this, it is postulated that air sacs in *Homo* were lost between 3.3 million and 500 thousand years ago, as shown by the presence or lack of the bulla in the fossil record. Further to this, there exists a statistically significant correlation between a reduction in body mass and the loss of air sacs in primates. Hewitt *et al.* (2002) demonstrate, using a synchronic analysis, that *Homo sapiens* is an exception to this trend. Language may be a justification for this, as the loss of air sacs has been suggested as being part of the general change in the vocal tract due to selection for linguistic production (Tomasello and Bates 2001),

However, I will present evidence against using the loss of the bulla as an argument for the cooccurrence of loss of air sacs in *Homo*. This leaves the dating of the loss of air sacs open. I will then go on to suggest that the Hewitt *et al.* (2002) study of body mass reduction and air sac loss, where *Homo sapiens* was an exceptional case, did not fully account for the lineage of current hominins. Using a diachronic analysis of hominin species, it is possible that *Homo* sapiens are not an exception to this correlation. This would mean that linguistic adaption may not have been significant factor in the loss of laryngeal air sacs in modern anatomical humans.

2 Morphological History

Air sacs are cavities that are attached to the vocal apparatus. They are present in many mammals (Frey et al., 2007), but only lateral ventricle air sacs occur in the ape line (Hewitt et al., 2002). Homo sapiens no longer have air sacs, except in rare pathological cases and in certain specific circumstances involving irregular behaviour-caused modification of the vocal tract.

There are several reasons that have been suggested for the loss of air sacs. For instance, air sacs are prone to a common ailment called 'airsacculitis': infection of the air sac. This is often posited as a pressure for the loss of air sacs in mammals – however, the lack of a cross-species study of the functions and uses of air sacs, particularly prior to being lost, has not yet been done (Hewitt *et al.* 2002). Other justifications given in the literature include the ability to modify breathing patterns and reduce need for a device that would prevent hyperventilating (Hewitt *et al.*, 2002). MacLarnon and Hewitt (1999) similarly suggest that the loss of air sacs may be beneficial towards fine breathing control, which is also necessary for modern human speech.

A linguistic justification is given by de Boer (to appear), who argues using a computer model that there is selection against air sacs as they are disadvantageous for subtle, timed, and distinct sounds, which are necessary for human speech. However, they may be advantageous for paralinguistic noises such as booms or other pre-linguistic calls similar to the chimp pant hoot: a lower F0 is more beneficial than fine control in male-to-male competition, which often drives the descent of the larynx in other species (Fitch and Reby, 2002).

3 The Bulla

A reliable indicator of the presence of air sacs in *Homininae* has been taken to be the bulla, which is a small extension of the hyoid bone that allows for the attachment of the laryngeal air sac to the vocal tract (de Boer, to appear, *and references therein*.) Fossilised hyoid bones of *Homo sapiens, neanderthalensis,* and *heidelbergensis* lack a clear bulla (Martínez *et al.*, 2008), but is present in *Austrolopithecus afarensis* (Alemseged *et al.*, 2006) This data has led to suggestions that the loss of the laryngeal air sac must have occurred between 3.3mya and 500kya (de Boer, to appear). It is impossible to fine-tune the date more than this based on the hyoid bone, as there are none extant (at the time of publication) in the archaeological record from *Austrolopithecus afarensis* to *Homo heidelbergensis*, a gap of 2.8 million years.

The loss of air sacs may have occurred more recently, as the loss of the bulla in the hyoid bone does not necessarily exclude the possibility of non-vestigial airs sacs, as laryngeal air sacs can regularly project between, reposition, and herniate muscles in the larynx (Giovanniello *et al.*, 1970). In primates, "A maximum of four types of [laryngeal] air sac (lateral ventricular, subhyoid, infraglottal and dorsal) have been identified, but no single source describes the morphology and summarises the distribution of all the types of air sac." (Hewitt *et al.*, 2002; 71) These four types occur in different species, but there are individual differences in air sac morphology, as well.

Laryngocoeles (non-fully formed or species-regular air sacs) can occur in pathological cases in humans. They can occur congenitally, or be acquired later in life. In such cases, the impetus is often due to an excessive build up in pressure in the glottis, which stretches the internal

wall to form a sac. This has been reported most in trumpet players, glass blowers, and other professionals who depend on pressure in the glottis. Internal pouches can block the vocal tract and result in hoarseness of breath and speech defects, but the air sacs can also herniate the surrounding tissue and sit between the muscles and the skin, creating a bulge (Giovanniello *et al.*, 1970). This bulge is a regular feature in other primate species, as seen in the non-pathological case of the Siamang *Symphalangus syndactylus* in Figure 1.

Figure 1 : Siamang air sac bulge



In some cervids, such as the Mongolian gazelle *Procapra gutturosa*, bulges (here the larynx) are part of the regular species morphology, but are not reflected in the bulla of the hyoid bone (Frey and Gebler, 2003; 460). The fact that vestigial air sacs occasionally occur in humans, along with the possibility for sacs to herniate the locale and vary between individuals, suggests that the lack of a hyoid bulla alone cannot adequately excuse a species from having air sacs, especially when considering that the bulla and air sacs need not disappear simultaneously, as bone and muscle morphology is little understood diachronically, and as there has been no detailed cross-species study of air sac morphology and use (Hewitt *et al.* 2002).

Furthermore, a major study looking at air sacs in primates in order to judge the acoustic effect of air sacs on call duration found that the bulla can exist in some species, but not in others, regardless of the presence of air sacs (Hewitt *et al.* 200). They note that the ancestral line of primates was likely to have had air sacs. This suggests that current bone morphology may be vestigial of previous states. But as Lovejoy (2009, p. 74e8) noted,

"There is no correlation between hyoid inflation and the presence or absence of air sacs in primates. For example, *Cercopithecus aethiops* lacks air sacs, whereas *Cercopithecus mitis* exhibits them. We have observed that the hyoid bodies of both species are equally inflated."

In light of this, and in light of the evidence provided above regarding air sac morphology, the presence of the bulla cannot be taken as irrefutable evidence of air sacs being present. The dating of the loss of air sacs therefore becomes an open question.

4 Size Reduction and Air Sac Loss

Hewitt *et al.* 2002 found a significant correlation between body size and presence of air sacs in primates, looking at 18 divergent cases. However, they performed a synchronic study, and so did not control for evolutionary changes that might have occurred after a split between a

species with sac and one without (such as, for instance, *Homo sapiens* and *Pan.*) There were four exceptions to this correlation – *Homo sapiens* being one of them.

"The exceptions were the evolution of *Microcebus murinus*, *A. trivirgatus*, *Callicebus molloch* and *Homo sapiens*, the first 3 species having evolved sacs without an increase in body weight (2 negative contrasts and 1 zero contrast) and human evolution involved an increase in body weight and the loss of air sacs (negative contrast)." (Hewitt *et al.* 2002, p. 79)

However, this is dependent on a steady, continual increase in average body size from *Homininae* to *Pan* and *Homo*. This is not the case; as early as 40kya *Homo sapiens* were significantly larger than modern population (in some cases) (Hermanussen *et al.*, 2003). There was a marked decrease in size from *Homo heidelbergensis* to *Homo sapiens* (Although not from *Homo ergaster* to *Homo heidelbergensis*) (Soligo *et al.*, 2006). This suggests that using the weight measurements of living species as a justification for the loss of air sacs despite a gain in body mass is unfounded given paleontological evidence, which suggests that it is possible that the laryngeal air sacs may have been lost only after size reduction in *Homo sapiens* from *Homo heidelbergensis*, or that it alternatively may have been lost during a state of relative stasis in total body mass between *Homo ergaster* and *heidelbergensis*.

5 Conclusion

If it is the case that the lack of a bulla in *Homo heidelbergensis* does not necessarily indicate lack of laryngeal air sacs, and that body size in *Homo* correlate with other losses, then the environment in which this change may have occurred must be examined. It is possible that the change in environment from forest to grassland may have been significant, or that other functional aspects of the breathing apparatus may have influenced the loss of air sacs in *Homo sapiens*. More studies on how environmental acoustics, in particular in evolutionary settings, affect anatomical changes remains an exciting area for future research on other possible justifications for air sac loss.

There is also other work that is needed on this topic. There has been to date few detailed published studies of air sacs across a wide variety of species and orders, either morphologically or based on their usage. There is little research into the evolution of air sacs or their disappearance. There have been few studies on hyoid bones outside of primates regarding air sacs, as most hyoid studies tend to focus on the position of the larynx. Additionally, there are few evolutionary archaeological findings of hyoid bones, as it is one of the smallest, and the only unconnected bone in the body. It may yet be correlated to air sacs in the *Homo* line, but currently there is no conclusive proof that this is the case. As well, studies are necessary regarding breathing regulation involving air sacs, and there is a dearth of morphological research into this area, although there has been extensive modeling (de Boer, *to appear*).

It is hoped that study into these areas will provide illumination on the situation involving air sacs in the *Homininae* lineage. In turn, this will contribute to understanding how language has shaped, and will contribute to shape, the anatomy of *Homo sapiens*.

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