

Re-Dating the Loss of Laryngeal Air Sacs in *Homo sapiens*

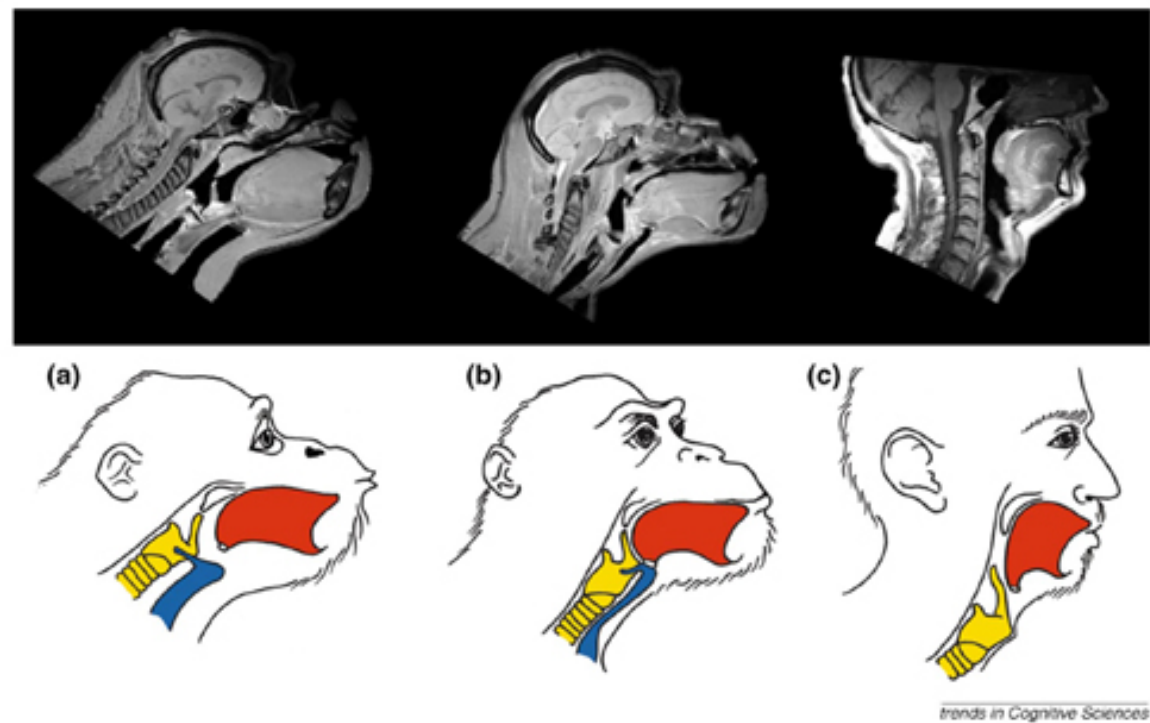
The Question

Air sacs are found in a wide variety of different animals; in mammals, they appear in bats, cetaceans, ungulates, and many other species. Laryngeal air sacs, which are situated above the vocal chords, appear in many primates – including all of the apes, excepting *Homo sapiens*. Differences in the hyoid bone between *Homo sapiens* and various hominin ancestors, such as *Australopithecus afarensis*, point to the loss of air sacs. So, why is it that *Homo sapiens* do not have air sacs? And when did this occur – did it happen soon after *Australopithecus afarensis*, around 3mya, or closer to *Homo sapiens*, around 500kya?

Here, I present two arguments that place the date of the loss of laryngeal air sacs closer to *Homo sapiens* than has currently been considered: one argument defends laryngeal air sac presence despite no evidence of a bulla in the hyoid bone; the other argument suggests that previous studies finding a significant correlation between a growth in body size and retention of air sacs in primates, (with the exception of *Homo sapiens*) did not fully account for the lineage of current hominins.

I then present two alternative justifications for the loss of air sacs: firstly, the evolutionary emphasis on directionality of calling in a savannah-like environment, and secondly, on the reuse of air in heavy breathing as being disadvantageous to extended exercise, and therefore a selective pressure against air sacs in hunting cultures.

Laryngeal Air Sacs: Morphological History

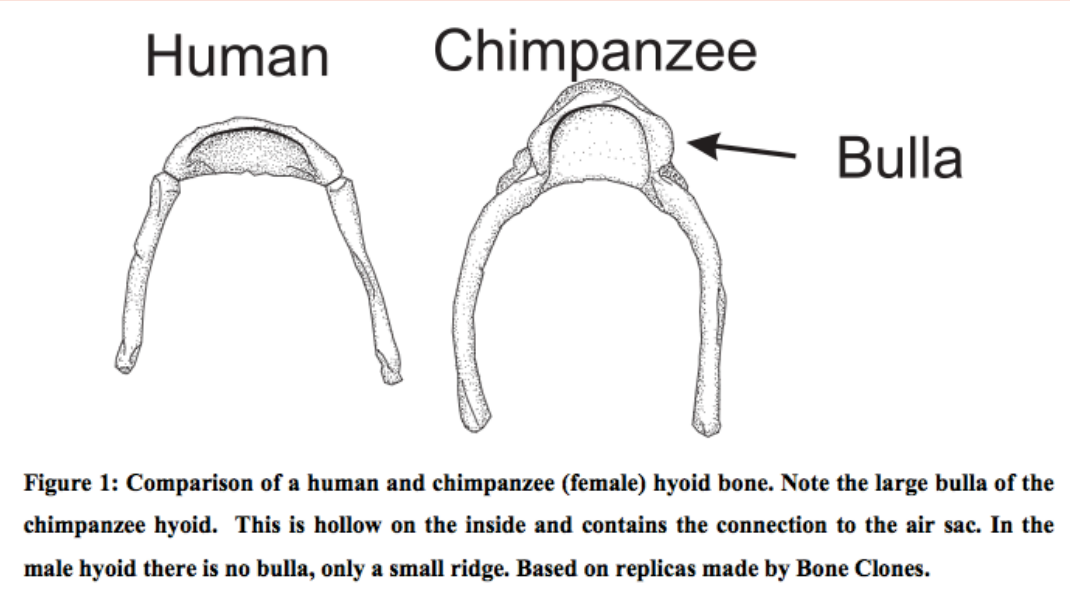


Air sacs are cavities that are attached to the vocal apparatus. They are present in many mammals (Frey *et al.*, 2007), but only lateral ventricle air sacs occur in the ape line (Hewitt *et al.*, 2002). *Homo sapiens* no longer have air sacs, except in rare pathological cases and in certain specific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

The vocal track structure, with air sacks in blue, of an an orangutan, chimpanzee, and human are presented to the left. An example of a bulla is given below (de Boer, 2010).

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 sack to the vocal tract (de Boer, 2010, *and references therein*.) A bulla is lacking in fossilised hyoid bones of *Homo sapiens*, *neanderthalis*, and *heidelbergensis* (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, 2010).

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. Thus, other justifications are given in the literature; in particular, the ability to modify breathing patterns and reduce need for a device that would prevent hyperventilating (Hewitt *et al.*, 2002).



A linguistic justification is given by de Boer (2010), 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 are advantageous for paralinguistic noises such as booms: a lower F0 is more beneficial than fine control in male-to-male competition. 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.

Arguments for Re-Dating Loss

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 air 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. In such cases, the impetus is often due to 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 (as seen in the non-pathological case of the Siamang *Symphalangus syndactylus*, above) (Giovanniello *et al.*, 1970). 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). Vestigial air sacs occasionally 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.

Further, 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. However, this is dependent on a steady, continual movement from *Homininae* to *Pan* and *Homo*. This is not the case; as early as 40kya there were considerable body size differences in human populations from today's population (Hermanussen *et al.*, 2003). There was also 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 the weight measurements of living species as a justification for the loss of air sacs despite a gain in body mass is unfounded given archaeological 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*.

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.

Arguments for Loss

I suggest two further possible, scenario-based reasons (loosely situated within the hunting hypothesis framework) for the loss of the laryngeal air sacs in *Homo sapiens*. First, the linguistic niche of hunting in the environment in which early hominin hunters (around 1.8mya) have been posited to exist - the savannah - would have been better suited to higher frequency, directional calls as opposed to lower frequency, multidirectional calls.

“However, the habitat of *P. gutturosa* ... is devoid of higher vegetation. In such an environment an almost undisturbed sound propagation around the head of a vocalizing animal can be assumed. The lower the emitted frequency, the more homogeneous is the directivity of the call (Gebler, 2001). Therefore, in the habitat of *P. gutturosa* a call with a low pitch may be best suited for multidirectional advertisement calls during the rut (Bradbury & Vehrencamp, 1998).” (Frey & Gebler, 2003; 469)



As in the case with rutting Mongolian antelope *P. gutturosa*, the advent of targeted communication would have been beneficial to the signallers, as the reduction of extraneous noise would have been disadvantageous towards any excluded party, which would not be able to hear or interpret the utterance. (This would most aptly refer to prey, but could also to apply to any present conspecifics.) The loss of air sacs would have then been directly advantageous, as lower frequencies produced by air sac vocalisations over bare ground have been shown to favour multidirectional over targeted utterances (Frey and Gebler, 2003; 469).

Secondly, the reuse of air stored in air sacs could have possibly been disadvantageous toward sustained, regular heavy breathing, as would occur in a similar hunting environment. Laryngeal ventricular air sacs, as seen in apes, open into the vocal tract above the vocal folds. This means that, as air is passed into the lungs, air is drawn from the sac, and as it is exhaled, the sac fills with air. For this reason, the reuse of air has been speculated to function as an anti-hyperventilating device used with irregular breathing patterns to stabilise the amount of oxygen, much as a brown paper bag can be used by humans during a panic attack (Hewitt *et al.*, 2002; 84).

This may be true for primates and other air sac bearers which do not perform long distance exercises; however, hominins with linguistic abilities must be able to control breathing mechanisms, and so this block would become superfluous. With the advantage of air sacs for this purpose made redundant, the air sac would serve as a sink of already-used air that would continually be reused while breathing, an inefficient mechanism that would be disadvantageous in cases of sustained oxygen depletion.

More work, hopefully of the experimental nature, is necessary before either of these two conjectures can be validated.

Challenges & Future Directions

More work is needed on this topic. There has been to date no published study of air sacs across species, 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: for example, hyoid bones are not extant in the archaeological record from *Austrolopithecus afarensis* to *Homo heidelbergensis*.

More studies on the biolinguistic environment are called for – how environmental acoustics, in particular in evolutionary settings, affect phonetics remains an open question . As well, studies are necessary regarding breathing regulation involving air sacs, as only one computational model this author is aware of currently exists, and there is a dearth of morphological studies (de Boer, 2010).

It is hoped that study into these areas will provide illumination on the situation involving air sacs in the *Homininae* lineage.

References

Alemseged, Z., Spoor, F., Kimbel, W. H., Bobe, R., Geraads, D., Reed, D., et al. (2006). A juvenile early hominin skeleton from Dikika, Ethiopia. *Nature*, 443(7109), 296–301.

Boer, B. de. (to appear). Air sacs and vocal fold vibration: Implications for evolution of speech.

Bradbury JW, Vehrencamp SL (1998) Principles of Animal Communication. Sunderland, MA: Sinauer Associates.

Fitch, T. (2006). Production of Vocalizations in Mammals. *Encyclopedia of Language and Linguistics*. Elsevier.

Frey, R, & Gebler, A. (2003). The highly specialized vocal tract of the male Mongolian gazelle (*Procapra gutturosa* Pallas, 1777–Mammalia, Bovidae). *Journal of anatomy*, 203(5), 451-71. Retrieved June 1, 2011, from <http://j.usa.gov/jr654k>

Frey, R., Gebler, A., Fritsch, G., Nygrén, K., & Weissengruber, G. E. (2007). Nordic rattle: the hoarse vocalization and the inflatable laryngeal air sac of reindeer (*Rangifer tarandus*). *Journal of Anatomy*, 210(2), 131-159. doi: 10.1111/j.1469-7580.2006.00684.x.

Gebler A (2001) Richtcharakteristik der Lautgebung beim Haushund (*Canis Lupus f. familiaris*). Diploma Thesis, Hum- boldt Universität, Berlin.

Giovanniello, J., Vincent Grieco, R. & Bartone, M. F. (1970). Laryngocoele. *American Journal of Roentgenology* 108, 825-829.

Hermanussen, M. (2003). Stature of early Europeans. *Hormones* (Athens, Greece), 2(3), 175-8. Retrieved June 9, 2011, from <http://www.ncbi.nlm.nih.gov/pubmed/17003019>.

Hewitt, G., MacLarnon, A., & Jones, K. E. (2002). The functions of laryngeal air sacs in primates: a new hypothesis. *Folia primatologica international journal of primatology*, 73(2-3), 70-94. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12207055>.

MacLarnon A.M., Hewitt G.P. (1999). The evolution of human speech: The role of enhanced breathing control. *Am J Phys Anthropol*, 109:341–363.

Martínez, I., Arsuaga, J. L., Quam, R., Carretero, J. M., Gracia, a, & Rodríguez, L. (2008). Human hyoid bones from the middle Pleistocene site of the Sima de los Huesos (Sierra de Atapuerca, Spain). *Journal of human evolution*, 54(1), 118-24. doi: 10.1016/j.jhevol.2007.07.006.

Soligo, C. (2006). Correlates of body mass evolution in primates. *American journal of physical anthropology*, 130(3), 283-93. doi: 10.1002/ajpa.20298.