
Hypoglossal Canal Size in Living Hominoids and the Evolution of Human Speech

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Abstract The relative size of the hypoglossal canal has been proposed as a useful diagnostic tool for the identification of human-like speech capabilities in the hominid fossil record. Relatively large hypoglossal canals (standardized to oral cavity size) were observed in humans and assumed to correspond to relatively large hypoglossal nerves, the cranial nerve that controls motor function of the tongue. It was suggested that the human pattern of tongue motor innervation and associated speech potential are very different from those of African apes and australopithecines; the modern human condition apparently appeared by the time of Middle Pleistocene *Homo*. A broader interspecific analysis of hypoglossal canal size in primates conducted in 1999 has rejected this diagnostic and inferences based upon it. In an attempt to resolve these differences of opinion, which we believe are based in part on biased size-adjustments and/or unwarranted assumptions, a new data set was collected and analyzed from 298 extant hominoid skulls, including orangutans, gorillas, chimpanzees, bonobos, siamang, gibbons, and modern humans. Data on the absolute size of the hypoglossal nerve itself were also gathered from a small sample of humans and chimpanzee cadavers. A scale-free index of relative hypoglossal canal size (RHCS) was computed as $100 \times (\text{hypoglossal canal area}^{0.5} / \text{oral cavity volume}^{0.333})$. No significant sexual dimorphism in RHCS was discovered in any species of living hominoid, but there are significant interspecific differences in both absolute and relative sizes of the hypoglossal canal. In absolute terms, humans possess significantly larger canals than any other species except gorillas, but there is considerable overlap with chimpanzees. Humans are also characterized by large values of RHCS, but gibbons possess an even larger average mean for this index; siamang and bonobos overlap appreciably with humans in RHCS. The value of RHCS in *Australopithecus afarensis* is well within both human and gibbon ranges, as are the indices computed for selected representatives of fossil *Homo*. Further-

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more, the size of the hypoglossal nerve itself, expressed as the mass of nerve per millimeter of length, does not distinguish chimpanzees from modern humans. We conclude, therefore, that the relative size of the hypoglossal canal is neither a reliable nor sufficient predictor of human-like speech capabilities, and paleoanthropology still lacks a quantifiable, morphological diagnostic for when this capability finally emerged in the human career.

“I am almost convinced that the evolution of human language went through a stage of learned, laryngeal vocalizations, which could be comparable to the communication systems of some birds, and furthermore that this stage occurred after the separation from the pongids and thus at approximately the australopithecine stage” (Livingstone 1973).

Some three decades after Livingstone offered his predictions about the nature and timing of human speech evolution, paleoanthropology still lacks a consensus on precisely when articulate speech and language emerged in the human career (Fitch 2000). Although language and speech are not the same things, speech is the specific auditory-vocal medium used by humans to convey our language. Since it seems likely that we will never discover the first fossilized words, the evidence for human-like speech capabilities is necessarily sought in the comparative analysis of morphology. Endocasts have been scrutinized for reorganization of the brain (e.g., Holloway 1974; LeMay 1975; Falk 1980; Aiello and Dean 1990), cranial base flexion has been measured and linked to hyoid position [e.g., Lieberman and Crelin 1971; Laitman and Heimbuch 1982; cf. Lieberman and McCarthy (1999) for a critique], and size of the thoracic vertebral canal has been evaluated with an eye towards spinal cord function and control of expiratory musculature (MacLarnon and Hewitt 1999). Regrettably, we concur with Fitch (2000:262–263) that these efforts have failed thus far to provide a consistent and convincing link between those aspects of anatomy and the origins of human speech: “despite an extensive and disputatious literature, most potential fossil cues to phonetic abilities appear inconclusive, suggesting that it will be difficult to reconstruct the vocal behavior of our extinct ancestors with any certainty.”

Kay et al. (1998) and Cartmill (1998) offered a promising new morphometric diagnostic for speech based on the relative size of the hypoglossal canal. It was reasoned that one should expect enhanced motor control of the tongue musculature with the emergence of human-like speech and language. It followed logically that an increase in the ratio of motor neurons to tongue muscle fibers might serve to signal when a level of human-like vocal control and speech was achieved. To this end, the relationship between the size of the hypoglossal nerve and the size of the tongue could be estimated via osteological surrogates for both extant species and some fossil hominids of known antiquity. Based on an analysis of the size of the hypoglossal canal (the hypoglossal nerve surrogate) in relation to size of the oral cavity (the tongue surrogate), Kay et al. (1998) concluded that early Plio-pleistocene hominids had quite small hypoglossals comparable to living African apes, and therefore probably lacked modern human-like speech capabilities.

However, it was suggested that modern lingual abilities were still quite ancient, dating perhaps as far back as 300,000 years BP, “much earlier than has been inferred from the archeological evidence for the antiquity of symbolic thought” (Kay et al. 1998:5419).

DeGusta et al. (1999) soon challenged the hypoglossal diagnostic and related inferences about speech potentials. Their extant comparative sample was broader in taxonomic terms, and within it they discovered extensive overlap in the absolute and relative sizes of the hypoglossal canal among humans, various anthropoid species and some australopithecines. Humans were shown to be extremely variable in size of the hypoglossal canal. These authors also questioned the strength of the relationship between canal and nerve size, finding a weak, non-significant correlation between the two in a small sample of human cadavers. Australopithecines were found to “have hypoglossal canals that, both absolutely and relative to oral cavity volume, are equal in size to those of modern humans” (DeGusta et al. 1999:1800). They concluded that the size of the hypoglossal canal does not reliably mirror vocal capacity or language usage, and the date for the emergence of human language was still open to question.

To their critique of Kay et al. (1998), one might also add a caveat with respect to using residuals from an African ape baseline as the measure of “relative” hypoglossal canal size (Jungers et al. 1995). This “line-of-subtraction” procedure assumes implicitly that the differences among bonobos, chimpanzees, and gorillas in canal size relative to oral cavity size are merely size-required, allometric changes that preserve functional equivalence in nonspeaking apes. Unfortunately, the alternative size-adjustment of DeGusta et al. is also fraught with problems. Dividing hypoglossal area directly by oral cavity volume overcorrects the numerator and ignores simple dimensional rules of comparison. Geometrically identical animals of different size would necessarily have different ratios due merely to this mismatch in dimensionality. It is no surprise, then, to observe that small primates (e.g., the prosimians in their sample) appear to possess relatively large canals by virtue of this miscalculation. Other factors further complicate some of the conclusions reached by DeGusta et al. (1999). It is dangerous to generalize from a nonsignificant relationship within an intraspecific sample (i.e., humans) to the interspecific situation, because significant correlations can exist in the latter even when the same pair of variables are weakly associated in the former (see below).

In view of these starkly differing conclusions and the incommensurable diagnostics upon which they are based, the present study reevaluates the original Kay et al. hypothesis. New data are collected from a large sample of living hominoids, including lesser apes and orang-utans in addition to African apes and modern humans. Relative hypoglossal canal size is defined here as a scale-free, dimensionally sound index that makes no a priori assumptions about functional equivalence in subsets of the overall extant hominoid sample. Data are also presented that compare directly the size of the hypoglossal nerve in cadavers of chimpanzees and modern humans.

Materials and Methods

New hypoglossal canal replicas were made from a flexible, injectable molding material (President Jet, Coltene AG, Switzerland) in a sample of 298 living hominoids. The sample includes 55 adult gorillas (31 males, 24 females), 57 chimpanzees (26, 31), 31 bonobos (14, 17), 22 orang-utans (12, 10), 28 siamang (12, 12), 58 lar gibbons (32, 26), and 47 modern humans (sexes pooled). The gorilla, chimpanzee, orang, and lar gibbon samples combine individuals of different subspecies, but most of the gorillas are western lowland gorillas (*Gorilla gorilla gorilla*), most of the chimpanzees are *Pan troglodytes troglodytes*, and most of the gibbons are *Hylobates lar carpenteri*. The modern human sample is geographically diverse, including Andaman Islanders, Africans, Inuit, and individuals of unknown ethnic affinities; the human samples were pooled after testing for significant differences among groups revealed none. It is important to note that canal replicas were collected and measured only from individuals whose canals were undivided. This criterion excluded many male gorillas and many orang-utans that exhibited bilaterally septate hypoglossal canals.

All replicas were sectioned at the site of minimum cross-section within the canal and measured by one of us (AAP). Digital images of these sections were captured from a dissecting microscope mounted with a high-resolution digital video camera, and area of the canal section was calculated in mm² using either NIH Image or SigmaScan software. Oral cavity volume (mm³), the tongue surrogate, was calculated as the product of palate length, palate breadth, and (palate depth + mandibular corpus depth at the second molar) following Kay et al. (1998). Hypoglossal canal area and oral cavity volume were converted to linear dimensions and used in the calculation of a scale-free, dimensionless index of Relative Hypoglossal Canal Size (RHCS):

$$\text{RHSC} = 100 \times (\text{hypoglossal canal area})^{0.5} / (\text{oral cavity volume})^{0.333}$$

Means and standard deviations were calculated for raw hypoglossal canal size, oral cavity size, and RHCS. Both the Kruskal-Wallis nonparametric test statistic and single classification analysis-of-variance (ANOVA) were used to test for equality of species-specific sample means, and the Games & Howell post hoc test was used for pair-wise multiple comparisons following ANOVA (because variances were never found to be homogeneous across samples). We also present our results graphically as box-and-whiskers plots or as bivariate scatters with convex polygons around each species. The statistical association between hypoglossal canal area and oral cavity volume was assessed within and across species by the parametric correlation coefficient using both raw and logged data. SPSS version 11.0 was used for all calculations.

The hypoglossal nerve was dissected out unilaterally in adult cadavers of 11 humans and 2 common chimpanzees (*Pan troglodytes*). In each specimen, a section of the nerve, distal to the hypoglossal canal opening and proximal to the

Table 1. Hypoglossal Canal Area, Relative Hypoglossal Canal Size, and Oral Cavity Volume in Living Hominoid Primates

<i>Species</i>		<i>N</i>	<i>Hypoglossal</i>	<i>Relative</i>	<i>Oral Cavity</i>
			<i>Canal Area (mm²)</i>	<i>Hypoglossal</i>	<i>Volume (mm³)^b</i>
			<i>Mean (SD)</i>	<i>Canal Size^a</i>	<i>Mean (SD)</i>
Orang-utans	Pooled	22	9.21 (3.09)	4.77 (0.83)	260406 (89852)
	Females	10	8.37 (2.93)	4.93 (0.89)	196502 (42783)
	Males	12	9.91 (3.17)	4.63 (0.79)	313659 (84316)
Gorillas	Pooled	55	14.85 (6.10)	5.61 (1.17)	315697 (79300)
	Females	24	13.90 (6.30)	5.84 (1.32)	247479 (43690)
	Males	31	15.58 (5.94)	5.43 (1.03)	368511 (57014)
Chimpanzees	Pooled	57	11.57 (3.33)	6.31 (0.95)	155469 (26961)
	Females	31	10.62 (2.29)	6.13 (0.73)	150609 (24861)
	Males	26	12.69 (4.01)	6.52 (1.14)	161264 (28677)
Bonobos	Pooled	31	7.79 (3.01)	6.09 (1.15)	93106 (15640)
	Females	17	6.93 (2.53)	5.76 (0.98)	92737 (15816)
	Males	14	8.85 (3.30)	6.49 (1.25)	93554 (16006)
Siamang	Pooled	2	6.20 (1.82)	6.93 (1.00)	45383 (7165)
	Females	14	5.86 (2.05)	6.89 (1.28)	42134 (4045)
	Males	14	6.54 (1.56)	6.97 (0.67)	48629 (8220)
Gibbons	Pooled	58	6.77 (2.26)	9.22 (1.69)	21776 (3004)
	Females	26	6.38 (2.11)	9.09 (1.64)	20921 (2827)
	Males	32	7.09 (2.36)	9.34 (1.74)	22471 (3006)
Modern humans	Pooled only	47	17.84 (5.39)	8.83 (1.26)	107945 (21802)

a. Relative hypoglossal canal size = $100 \times (\text{hypoglossal canal area})^{0.5} / (\text{oral cavity volume})^{0.333}$.

b. Oral cavity volume = (palate breadth \times palate length \times [palate depth + corpus depth]).

junction of nerve XII with the superior ramus of the ansa cervicalis, was removed and preserved in 100% ethanol. From these sections, the cross-sectional area of the nerve was measured as mass in grams per millimeter of nerve length. On two of the human specimens, the region containing the hypoglossal canal was removed from the head on the undissected side and decalcified following the procedures described by Hildebrand (1968). The decalcified specimens were sectioned with a scalpel along a roughly coronal plane passing through the hypoglossal canal, thus revealing the canal's contents. Two other preserved human cadavers were dissected to examine the extracranial connections of the veins emerging from the hypoglossal canal.

Results

Descriptive statistics for hypoglossal canal area, relative hypoglossal canal area, and oral cavity volume are presented in Table 1. Following ANOVA, the Games & Howell post hoc test revealed that only oral cavity size exhibits any significant sexual dimorphism in our hominoid samples, with male gorillas being

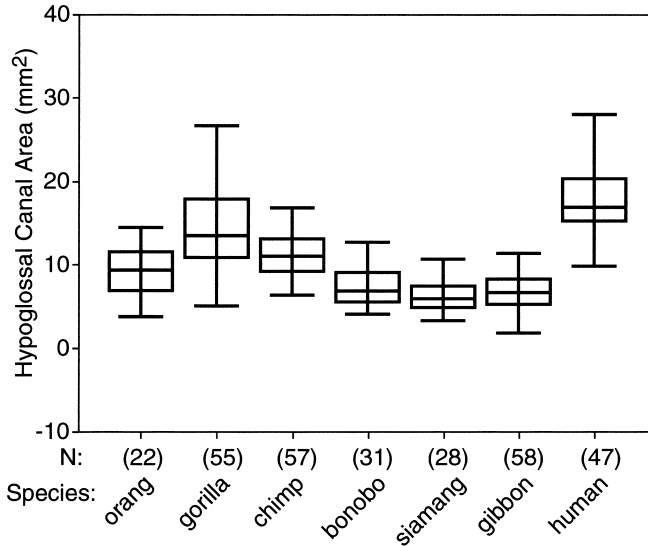


Figure 1. Box-and-whiskers plot of absolute hypoglossal canal size (in mm²) in living hominoids, sexes pooled within each species, adults only. The horizontal line is the median value, the box captures the central 50% of the data (interquartile range), and the whiskers include data within $1.5 \times$ the interquartile range; outliers are indicated by circles. There are significant differences among species, but humans and gorillas are not significantly different in this variable.

significantly larger than females ($p < 0.001$) and orang-utan males larger than females ($p < 0.05$). Neither absolute nor relative hypoglossal canal size were significantly sexually dimorphic ($p > 0.5$ in all comparisons); hence, sexes were pooled. Figure 1 displays variation among species in absolute size of the hypoglossal canal in a box-and-whiskers format (the horizontal bar is the median value, the box captures the central 50 per cent of the data, the whiskers encompass data that fall within $\pm 1.5 \times$ the interquartile range; and circles are outliers). Both Kruskal-Wallis and ANOVA confirm that there are significant differences among hominoid species in absolute size of the hypoglossal canal ($p < 0.001$), with humans, gorillas, and chimpanzees having the largest mean values. What is noteworthy here, however, is that the human value is not significantly different from that of the gorilla ($p > 0.1$), despite enormous differences in absolute body size and oral cavity size. This observation alone suggests that human hypoglossal canals are relatively large. However, chimpanzees and humans do overlap to a considerable degree.

Figure 2 is a scattergram of logged hypoglossal canal area versus logged oral cavity size. Convex polygons surround each species. Within each of the seven species examined here, there is no significant correlation between these two variables ($p > 0.05$ in all species), although $r = 0.4$ approaches significance in the orang-utans ($p = 0.07$). However, there is still a significant association between

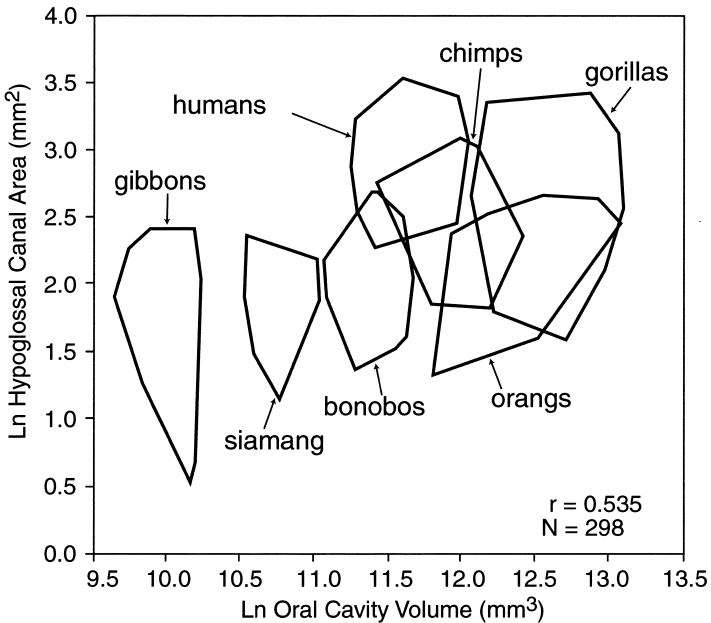


Figure 2. Bivariate scatterplot of Ln hypoglossal area versus Ln oral cavity size in living hominoids. A convex polygon is drawn around each species. Note the modest overlap between humans, chimpanzees, and bonobos. Correlations between these two variables are not significant within any of the species, but the interspecific correlation of $r = 0.535$ is statistically significant.

canal area and oral cavity volume across species ($r = 0.535$, $p < 0.01$). One cannot generalize from the intraspecific to interspecific in this and many other cases. Note the modest degree of overlap between chimpanzees and humans and between bonobos and humans.

Figure 3 illustrates interspecific variation in relative size of the hypoglossal canal (RHCS). Significant variation occurs among extant hominoid species ($p < 0.001$ for both Kruskal-Wallis and ANOVA). Orang-utans have the lowest values for RHCS. Chimpanzees have significantly larger RHCS than do gorillas ($p < 0.05$), but are not distinguishable in this regard from siamang ($p > 0.1$). Humans and lar gibbons have the largest values of RHCS by far, and they are not significantly different from one another in this respect ($p > 0.8$).

Figure 4 plots relative size of the hypoglossal nerve itself in chimpanzees ($N = 2$) and humans ($N = 11$). Mass of the hypoglossal nerve (grams) per unit length (mm) is variable in humans, and the two chimpanzees fall comfortably within the human range.

In the sectioned human specimens, bundles of nerve XII occupied a smaller percentage of the canal's cross-sectional area than was occupied by the accompanying vasculature (Figure 5). The hypoglossal venous plexus was the largest

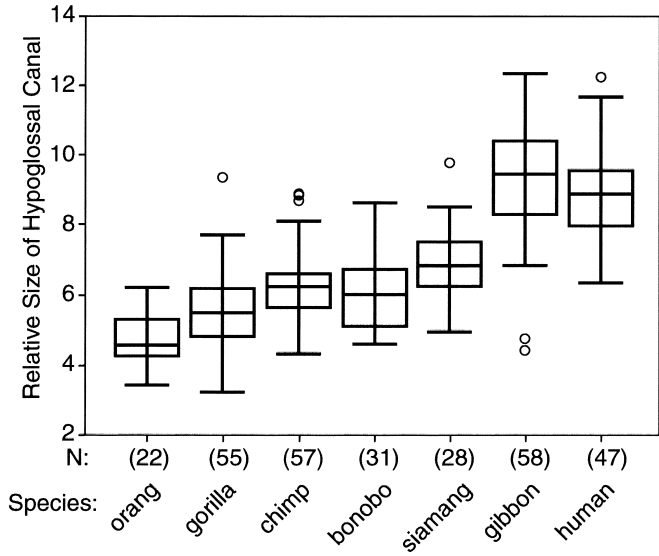


Figure 3. Box-and-whiskers plot of relative hypoglossal canal size (RHCS) in living hominoids. See text and Table 1 for the definition of RHCS. Orang-utans have the relatively smallest hypoglossal canals, the chimpanzee RHCS average is significantly greater than that of the gorilla, and humans and gibbons are characterized by the largest mean values of RHCS (and do not differ significantly from one another).

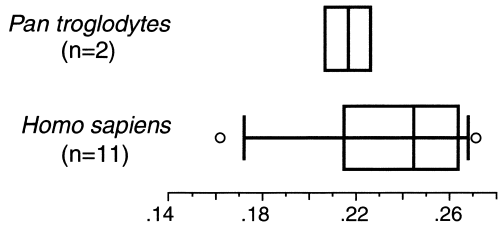


Figure 4. Box-and-whiskers plot of hypoglossal nerve size in two chimpanzee wet specimens and eleven human cadavers. Nerve mass per millimeter of nerve length does not serve to distinguish chimpanzees from humans.

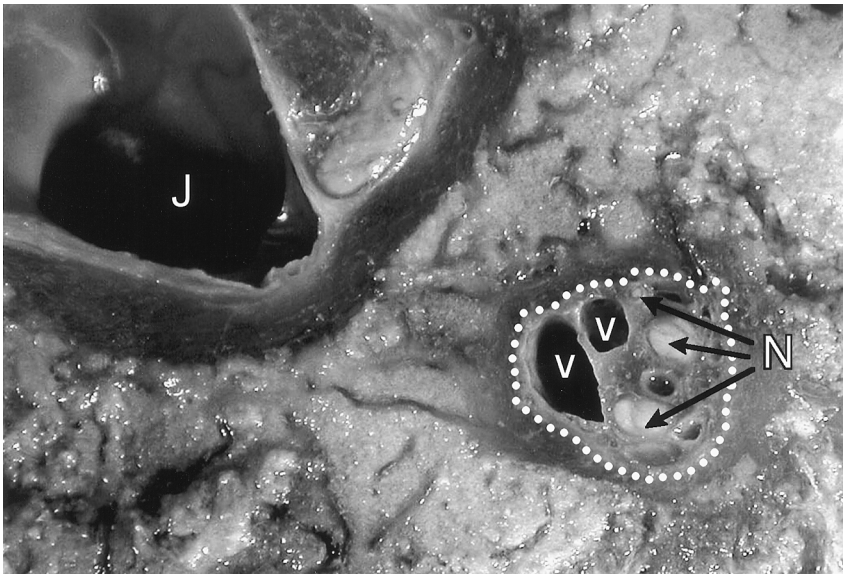


Figure 5. Vertical (approximately coronal) section through the hypoglossal canal in a human cadaver. The white dotted line outlines the lumen of the bony canal. **J**, bulb of the internal jugular vein; **V**, veins of the hypoglossal plexus; **N**, bundles of hypoglossal nerve within canal.

single constituent of the contents of the hypoglossal canal. Dissection of two cadavers showed the veins of the plexus coalescing into a single large channel that emerged from the opening of the canal and ran laterally to enter the upper end of the internal jugular vein just below the skull. In some human skulls, the hypoglossal canal is connected to the jugular foramen via a separate passage in the occipital bone. In life, this passage presumably transmitted a vein that emptied into the internal jugular vein or the lower end of the sigmoid sinus.

Discussion

The size of the hypoglossal canal is indeed relatively large in humans when compared to that in African apes (Kay et al. 1998), although overlap is apparent regardless of whether residuals or a scale-free index is used to capture this relationship. It seems correspondingly unlikely that the overlap is an artifact of imperfect adjustment for size differences (Kay et al. 1998). The data presented here and the measurements of human cadaveric canals and nerves reported by DeGusta et al. (1999) lead us to conclude that the average differences observed between humans and apes in canal size reflect differences in the relative size of the vascular or connective-tissue contents of the canal. Even if cross-sectional areas of the canal accurately reflected those of the hypoglossal nerve, the overlap found be-

tween chimpanzees and humans would preclude using canal size as a reliable indicator of articulate speech.

The finding that gibbons and humans possess similar values for RHCS also undermines the hypoglossal diagnostic for speech per se. Gibbons (and siamang) do possess complex vocal repertoires and have been described to “sing” and duet (Geissmann 2000, 2002), but to our knowledge they have never been reported to speak. It is tempting to suggest that the similarity between humans and gibbons is therefore a type of convergence due to different sorts of vocal virtuosity, but this inference is complicated by the fact that siamang also sing and duet but do not exhibit the exceptionally high values of RHCS seen in either gibbons or humans (Geissmann and Orgeldinger 2000).

For those who favor empirical lines of subtraction over geometrical criteria and ratios, it is perhaps worth noting that an examination of hypoglossal canal size residual to oral cavity volume leads to the same conclusions. More specifically, if hypoglossal canal residuals are calculated for all seven hominoid taxa using African apes as the line of subtraction (Kay et al. 1998) based on the reduced major axis (because extrapolation is required; Ricker 1984), gibbons and humans still possess the largest values on average and do not differ significantly between each other ($p > 0.6$).

Figure 6 adds four fossil hominids to the plot of RHCS: *Australopithecus afarensis* (using the data on a reconstruction of A.L. 333-45 from DeGusta et al. 1999), Skhul 5, Kabwe, and LaFerrassie (all three *Homo* from Kay et al. 1998). Note that all four fossils are very similar to each other and fall within the interquartile ranges of both humans and gibbons, and all four overlap the African apes and siamang at their respective extremes. If these fossils are representative of their species, then there appears to have been relatively very little change in hypoglossal canal/oral cavity proportions over the last three million years of the human career.

To summarize and conclude, we note that there is overlap in the envelopes of covariation between absolute hypoglossal canal size and oral cavity size in chimpanzees, bonobos, and humans. Although humans do possess relatively large hypoglossal canals in comparison to most apes, they are not significantly different from gibbons, and they imbricate to varying degrees in this respect with all living hominoids except the orang-utan. Fossil hominids (from *Australopithecus afarensis* to early *Homo*) that span some three million years of human evolution are remarkably similar to one another in the relative size of their hypoglossal canals, and all fall well within the ranges of variation seen in gibbons and humans, as well as at the extremes of variation seen in chimpanzees, siamang, and bonobos. The size of the hypoglossal nerve itself also does not serve to sort chimpanzees from modern humans, and this suggests that other contents of the hypoglossal canal influence its size. Despite its intuitive appeal and logical foundation in motor control, the relative size of the hypoglossal canal ultimately fails as a reliable and sufficient diagnostic for speech capabilities and the emergence of language in

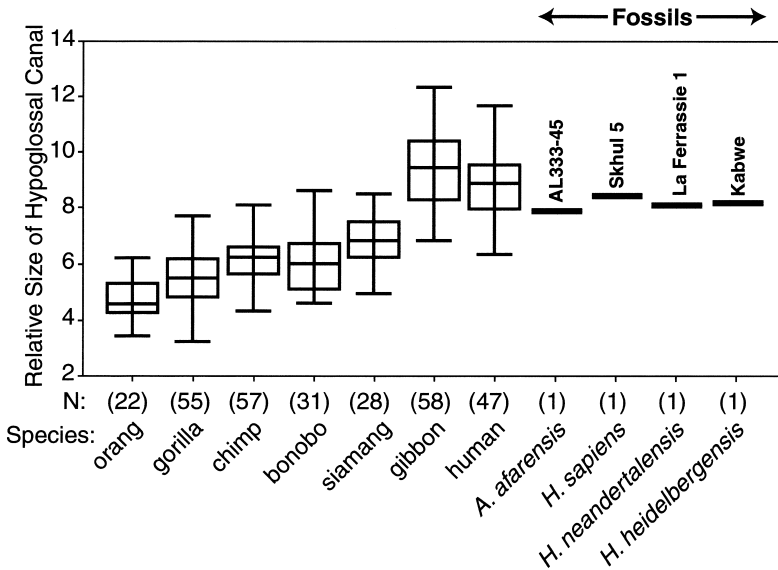


Figure 6. Box-and-whiskers plot of RHCS again with the addition of four fossil hominids: A.L. 333-45, Skhul 5, Kabwe, and LaFerrassie. All four fossils fall with the interquartile ranges of gibbons and humans and on the edges of variation in siamang, chimpanzees, and bonobos.

the fossil record of human evolution. To a large degree, therefore, we share the conclusions reached by DeGusta et al. (1999), but they were right mostly for the wrong reasons in view of their error in calculating relative size of the hypoglossal canal as a dimensionally biased ratio of an area to a volume.

Whether or not australopithecines (or Neandertals, for that matter) sang or spoke remains an open question for the moment. Perhaps Fitch (2000:263) is also correct in noting that morphological lines of inquiry into the timing of emergence of human speech and language have thus far “generated more heat than light, and diverted attention from alternative questions that are equally interesting and more accessible empirically,” namely, issues of how and why rather than when (e.g., loss of air sacs in humans, descent of the adult human larynx, acquisition of the ability to imitate novel sounds, and peripheral morphology versus neural control mechanisms in limiting nonhuman vocal production). The recent analysis of *FOXP2* differences between humans and other anthropoid primates (Enard et al. 2002) suggests that natural selection has targeted this gene related to articulation and the acquisition of normal spoken language; as such, it serves to remind us that we also still have very much to learn about the genetic substrate of speech and language at the molecular evolutionary level.

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