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Echoes from the past: New insights into the early hominin cochlea from a phylo-morphometric approach

Échos du passé : éclairages nouveaux sur la cochlée des premiers homininés par une approche phylo-morphométrique

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ABSTRACT

We investigate cochlear variation, an indirect evidence of auditory capacities among early hominins and extant catarrhine species, in order to assess (i) the phylogenetic signal of relative external cochlear length (RECL) and oval window area (OWA), (ii) the evolutionary model with the highest probability of explaining our observed data, (iii) some hominin ancestral nodes for RECL and OWA. RECL has a high phylogenetic signal under a Brownian motion model, and is closely correlated with body mass. Our model-based method has the advantage over parsimony-based methods of incorporating branch lengths in a phylo-morphospace, and this shows RECL shifted towards significantly higher values at the *Homo erectus-Homo sapiens* node. We also observe that the StW 53 and KB 6067 fossil specimens from Sterkfontein and Kromdraai likely represent one or two distinct, smaller-bodied and less derived hominin form(s) compared to *Paranthropus* specimens represented at Swartkrans.

RÉSUMÉ

Nous examinons la variation cochléaire, témoin indirect des capacités auditives des premiers homininés ainsi que d'espèces actuelles de catarrhiniens, afin d'évaluer (i) le signal phylogénétique de la longueur externe relative de la cochlée (RECL) et de la surface de la fenêtre ovale (OWA), (ii) le modèle évolutif montrant la plus forte probabilité d'expliquer

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nos observations, (iii) certaines valeurs ancestrales d'homininés pour RECL et OWA. RECL montre un signal phylogénétique élevé sous un modèle brownien, mais aussi une corrélation étroite avec la masse corporelle. Notre méthode, basée sur un modèle évolutif, présente l'avantage de tenir compte des longueurs de branches (contrairement aux méthodes cladistiques, basées sur la parcimonie) dans un espace phylo-morphologique soulignant une évolution de RECL vers des valeurs significativement plus élevées uniquement au nœud (*Homo erectus*, *Homo sapiens*). Nous observons également que les fossiles StW 53 et KB 6067 (provenant respectivement de Sterkfontein et de Kromdraai) représentent probablement une ou deux forme(s) d'homininé(s) de plus petite taille corporelle et moins dérivée(s), par rapport à *Paranthropus* représenté à Swartkrans.

1. Introduction

Amongst the five main sensory systems, the cochlea is the only organ that imprints details of its overall structure within bone; this takes the form of a spiral-shaped cavity housed by the petrosal part of the temporal. At least two features of this cavity can be determined and enable good estimates of the hearing capacities in fossil hominins: the relative external cochlear length (RECL) and the oval window area (OWA) (see Braga et al., 2013, 2015 for more details). For instance, cochlear length is taken as a proxy measure of a shorter basilar membrane length (with its sensors tuned to high frequencies at its base and lower frequencies progressively towards the apex), and was suggested to provide a good estimate of low-frequency hearing in non-human primates (Coleman and Colbert, 2010). One can therefore question how interactions of our hominin ancestors with environmental signals (i.e. habitat acoustics and vocalizations) may have played a role in the evolution of the unique low-frequency sensitivity displayed only by modern humans (i.e. *Homo sapiens sapiens*) among catarrhine primates (Coleman, 2009). This question is beyond the scope of the present study.

However, since cochlear features are useful in reconstructing the evolutionary history of auditory capacities among primates (Coleman and Colbert, 2010; Coleman et al., 2010), and show an association with phylogeny (Braga et al., 2015), we address two questions in this paper. First, can statistical procedures improve the detection of taxa that deviate significantly from general allometric equations (i.e. have larger or smaller cochlear features given their body size)? Second, can gross geometrical features of the cochlea in an unknown ancestral species be accurately predicted from knowledge of its phylogenetic nodal position? In order to address these issues, it is desirable to determine whether the cochlear geometrical variation observed among early hominins and other catarrhine species is phylogenetically meaningful (similarities indicating shared recent common ancestry) in possible relation to body size, and whether this can be tested according to different explicit evolutionary models (e.g., Brownian motion versus models with variable rates of evolution).

In a recent paper, Braga et al. (2015) used microfocus X-ray computed tomography (micro-ct) to measure the strength of RECL and OWA phylogenetic signals, and to determine whether some hominin species showed cochlear shifts for their body mass after correcting for gene-based phylogeny. It was concluded that RECL evolution in apes occurred mainly through body-mass-dependent and non-homoplasic changes. Moreover, both premodern and modern humans (*Homo erectus* and *H. sapiens sapiens*, respectively) showed RECL and OWA values larger than expected for their body mass (using phylogenetically controlled linear regressions), a condition not found in their non-human hominin predecessors (Braga et al., 2015). However, in that study, all the phylogenetic analyses assumed that Brownian motion was the best evolutionary model to explain the cochlear data observed among catarrhines. In a Brownian motion model of trait evolution, the expected phenotypic difference between sister species grows proportional to the time since they shared a common ancestor (i.e. the sum of the branch lengths between the two taxa) (Nunn, 2011). Given the available evidence that functional systems often do not evolve at constant rates but instead show strong positive selections (with accelerated evolutionary changes) (e.g., Clark et al., 2003), it is necessary to test whether RECL and OWA may have evolved following a non-Brownian model before attempting to reconstruct ancestral values.

Both RECL and/or OWA values have been investigated in *Australopithecus* (Sts 5, StW 329, StW 98, StW 255), *Paranthropus* (KB 6067, TM 1517, SK 879, SKW 18) and *H. erectus sensu lato* (or *H. ergaster*) (SK 847) (for more details, see Braga et al., 2013: Table 3; Braga et al., 2015: S1 table). However, since this study focuses mainly on phylogenetic issues, the KB 6067 specimen is treated separately from the Swartkrans *Paranthropus* sample because it has been preliminarily interpreted to "represent a more primitive condition for the *P. robustus* lineage, with more similarity to some Sterkfontein Member 4 specimens" (Braga et al., 2013: 455). Moreover, in the present study, we use only fossil specimens with both RECL and OWA values, hence allowing comparisons of the phylogenetic results for these two parameters by using the same samples. Therefore, Sts 5 and TM 1517 are excluded from our sample.

In addition to published data, the first aim of this study is to provide further RECL and OWA micro-ct measurements for three early hominin specimens from the Sterkfontein site (South Africa). The first, StW 498e has