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Description and analysis of three *Homo naledi* incudes from the Dinaledi Chamber, Rising Star cave (South Africa)

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ABSTRACT

This study describes three incudes recovered from the Dinaledi Chamber in the Rising Star cave system in South Africa. All three bones were recovered during sieving of excavated sediments and likely represent three *Homo naledi* individuals. Morphologically and metrically, the Dinaledi ossicles resemble those of chimpanzees and *Paranthropus robustus* more than they do later members of the genus *Homo*, and fall outside of the modern human range of variation in several dimensions. Despite this, when overall size is considered, the functional lengths in *H. naledi* and *P. robustus* are very similar to those predicted for a human with a similar-sized incus. In this sense, both taxa seem to show a relatively elongated functional length, distinguishing them from chimpanzees. The functional length in *H. naledi* is slightly longer in absolute terms than in *P. robustus*, suggesting *H. naledi* may already show a slight increase in functional length compared with early hominins. While *H. naledi* lacks the more open angle between the long and short processes found in modern humans, considered a derived feature within the genus *Homo*, the value in *H. naledi* is similar to that predicted for a hominoid with a similar-sized incus. Principal components analysis of size-standardized variables shows *H. naledi* falling outside of the recent human range of variation, but within the confidence ellipse for gorillas. Phylogenetic polarity is complicated by the absence of incus data from early members of the genus *Homo*, but the generally primitive nature of the *H. naledi* incudes is consistent with other primitive features of the species, such as the very small cranial capacity. These ossicles add significantly to the understanding of incus variation in hominins and provide important new data on the morphology and taxonomic affinities of *H. naledi*.

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1. Introduction

The three ossicles of the middle ear – the malleus, incus and stapes – have long been recognized as potential sources of phylogenetic information within primates (Hershkovitz, 1977; Coleman and Ross, 2004; Coleman and Colbert, 2010). This is due in part to the fact that these elements complete their growth in utero, do not remodel significantly after birth, and show little sexual dimorphism

(Kirikae, 1960; Scheuer and Black, 2000; Masali and Cremasco, 2006; Quam et al., 2014). In paleoanthropology, hominin ossicle morphology has been used to make inferences about hearing and perception, to study paleopathologies, and to shed light on taxonomy and phylogeny (Rak and Clarke, 1979; Masali et al., 1991; Moggi-Cecchi and Collard, 2002; Martínez et al., 2004; Crevecoeur, 2007; Quam and Rak, 2008; Martínez et al., 2013; Quam et al., 2013a,b; 2015; Gómez-Olivencia et al., 2015; Stoessel et al., 2016).

Despite their usefulness, auditory ossicles are easily overlooked or lost during the excavation and recovery of skeletal remains. As a result, they are particularly rare in the fossil record and research on them has been hampered by a paucity of specimens. To date, most

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of the specimens reported in the literature represent Middle or Late Pleistocene members of the genus *Homo* from Europe or Southwest Asia. Study of these specimens has revealed overall similarities in size between Neandertals and recent humans, including the functional length of the incus long process, as well as consistent anatomical differences that distinguish Neandertal ossicles from those of recent humans. In particular, the Neandertal incus shows a more closed angle between the long and short processes, a shorter distance between the tips of the long and short processes, a deeper and more asymmetrical interprocess curvature, a relatively straight long process, and a large articular facet (Heim, 1982; Quam et al., 2013a; Stoessel et al., 2016). Middle Pleistocene European specimens, considered broadly ancestral to the Neandertals, seem to show this same suite of features (Quam et al., 2006).

Two additional incudes are known from the site of Swartkrans in South Africa and have been attributed to *Paranthropus robustus* (Rak and Clarke, 1979; de Ruiter et al., 2002; Quam et al., 2013b). The incus in this taxon has been described as ape-like in showing small overall dimensions, an absolutely short functional length, and a more closed angle between the long and short processes (Quam et al., 2013b). While Middle and Late Pleistocene *Homo* specimens differ from early hominins in being larger overall, including the functional length of the long process, the closed angle between the long and short processes in Neandertal incudes seems to represent a primitive retention. However, there are currently no ear ossicles known from Middle Pleistocene African hominins to assess whether they show a similar morphology to Neandertals, or whether they differ along taxonomic lines. With such a limited fossil sample, particularly for Africa, any new material presents an opportunity to expand the geographic, temporal, and taxonomic breadth of comparative studies.

This study describes three incudes recovered from the Dinaledi Chamber of the Rising Star cave system, South Africa. To date, the chamber has yielded over 1700 hominin fossils, representing a minimum of at least 15 individuals (MNI = 15) attributed to the species *Homo naledi* (Berger et al., 2015; Dirks et al., 2015). This taxon shows a unique combination of primitive and derived features throughout the skull, teeth and postcranial skeleton (Berger et al., 2015; Harcourt-Smith et al., 2015; Kivell et al., 2015; Dembo et al., 2016; Feuerriegel et al., 2017; Garvin et al., 2017; Hawks et al., 2017; Laird et al., 2017; Schroeder et al., 2017; Marchi et al., 2017; VanSickle et al., 2018; Williams et al., 2017). This mosaic anatomy, combined with the very late dates (335–236 Ka) (Dirks et al., 2017), suggests that the evolutionary origin of *H. naledi* may be considerably earlier than the date of the assemblage and that the species persisted over a long geological period (Hawks and Berger, 2016).

Superficially, the incudes closely resemble each other and show little metric variation. All three have been attributed to *H. naledi* based on their context and the homogeneity of the skeletal assemblage within the chamber. By more than doubling the existing sample size of African incudes, the Dinaledi material contributes new data to questions about the structure and function of ear ossicles in hominins. In addition, it is becoming increasingly evident that the diversity and complexity of the human family tree has been underestimated (Brown et al., 2004; Arsuaga et al., 2014; Spoor et al., 2015; Stringer, 2016; Berger et al., 2017), and the analysis of these three elements has the potential to shed further light on the taxonomic affinities of *H. naledi*.

2. Materials and methods

2.1. Comparative samples

The three Dinaledi Chamber incudes were compared with a small, but taxonomically diverse, sample of fossil hominin ear

ossicles, including both early hominins and members of the genus *Homo*, as well as samples of modern humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla*) (Table 1). For the fossil hominins, most of the data were collected on scaled images of the original specimens, relying on the techniques outlined below. These were complemented by measurements reported in the literature (Stoessel et al., 2016).

The modern human sample ($n = 43$) derives from a large collection of ear ossicles removed during gross anatomy instruction and comprises non-pathological individuals of known sex and race ranging in age from 51 to 100 years old (Quam, 2006). The chimpanzee ($n = 47$) and gorilla ($n = 37$) samples are drawn from collections at several institutions, including the Cleveland Museum of Natural History (USA), American Museum of Natural History (USA), Academy of Natural Sciences of Philadelphia (USA), Estación Biológica Doñana (Spain) and the Universidad Complutense de Madrid (Spain) (Quam et al., 2014).

2.2. Measurement methodology

Measurements of the Dinaledi Chamber ossicles were taken on virtual reconstructions of the individual bones derived from microCT scans (see below). The virtual reconstructions of the individual ossicles were oriented in a similar fashion as those taken with a digital camera (Quam and Rak, 2008). The medial surface of the bone faced the viewer and the bone was oriented to expose the maximum length of the short and long processes in medial view. A scale was included in the image and a screenshot of the virtual reconstruction with the included scale was captured as a TIFF file. The 2D image was then opened, calibrated and measured in the PhotoshopTM software program, essentially replicating the measurement protocol for 2D digital images of the ossicles defined previously (Quam and Rak, 2008).

Measurement definitions follow Quam and Rak (2008). A series of seven linear measurements, one angular measurement, and two indices (Fig. 1; Table 2) were taken and calculated on each bone to capture the main metric aspects of the incus. Three axes (X, Y and Z) were identified on the incus, and used to orient the bone for measurement purposes. Two of these correspond to the main axes of the long and short processes (X- and Y-axes) and the third represents the rotational axis (Z-axis) of the incus when it is articulated within the ossicular chain.

2.3. Micro-CT scanning and virtual reconstruction

The micro-CT scanning of the *H. naledi* incudes was carried out at the University of the Witwatersrand's Microfocus X-ray Computed Tomography (CT) facility in Johannesburg, South Africa. Scanning was conducted using a Nikon Metrology XTH 225/320 LC dual source CT system, with scan parameters of 70–85 kV, 95–150 μ A, with a resolution which varied from 7.98 to 15.4 μ m. Virtual reconstruction of the *H. naledi* incudes was carried out using the Mimics™ v.17 (Materialise, Leuven, Belgium) software program.

2.4. Statistical analysis

Statistical analysis of the metric data was carried out using the Statistica™ software program. In addition to descriptive statistics, the metric data were subjected to principal components analysis (PCA). To control for size effects, the variables were first transformed by dividing by the geometric mean. PCA was carried out on the correlation matrix of the metric data. PCA reduces the number of variables to a smaller number of components whose constituent variables can then be analyzed. By default, PCA generates the same number of components as variables in the analysis, but only those

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