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Reassessment of the La Ferrassie 3 Neandertal ossicular chain

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ABSTRACT

The ossicular chain in La Ferrassie 3 was briefly described in the monograph on the La Ferrassie Neandertal children, but to date has not been the subject of detailed study. We provide new data on these important fossils and re-examine some previous suggestions of derived Neandertal features in the middle ear ossicles based on more limited evidence. The malleus shows a curved lateral margin of the manubrium and a relatively large head. The incus shows a tall articular facet, a depressed area on the medial surface of the body, a straight anterior border of the long process and a more closed angle between the processes. The stapes shows an asymmetrical configuration of the crura, with an anteriorly skewed head, and generally small dimensions, including a smaller and relatively wider stapedial footplate. These same features can also be seen in the few other Neandertal ear ossicles known, suggesting that a consistent anatomical pattern characterizes the Neandertal ossicular chain. While the phylogenetic polarity of many of these features remains to be clarified, the asymmetrical stapes and anteriorly skewed stapedial head appear to be derived Neandertal features. In addition, while the larger malleus head and incus articular facet in La Ferrassie 3 might reflect larger body mass in Neandertals, the larger stapes footplates in *Homo sapiens* cannot be explained by changes in body mass. Indeed, *H. sapiens* seems to depart from the general mammalian pattern in combining an increase in stapes footplate size with a decrease in body mass. Although the malleus/incus lever ratio in La Ferrassie 3 is similar to that in *H. sapiens*, Neandertals appear to be characterized by a slightly different spatial relationship and articulation of the ossicular chain within the tympanic cavity. While only limited inferences can be drawn regarding hearing ability based on the ossicles, the few physiologically relevant dimensions in the La Ferrassie 3 ear bones are similar to *H. sapiens*.

Introduction

The La Ferrassie 3 (LF3) Neandertal is one of the very few human fossil specimens to preserve a complete ossicular chain (malleus, incus and stapes). The bones were briefly described and a few metric dimensions were provided by Heim in the monograph on the La Ferrassie Neandertal children (Heim, 1982).[1] Heim suggested that the Neandertal ossicles were distinct from those of fossil and recent *Homo sapiens* in a number of subtle aspects. In particular, the malleus in LF3 was slightly longer, with a larger head and a more open angle between the manubrium and the head/neck. In addition, the manubrium was relatively straight with a well-developed lateral (short) process, the latter implying a greater protrusion of the tympanic membrane. The incus shows a longer long process, which is relatively straight and thin. In contrast, the short process is shorter and does not show a notch in its lower border. The articular surface is described as large and the body as slightly flatter than in *H. sapiens*. The stapes is slightly smaller and shows a pronounced asymmetry between the shorter anterior crus and the longer and more curved posterior crus. The head of the stapes is skewed anteriorly and the crura are thicker in LF3. In sum, the Neandertal ear ossicles are said to differ from *H. sapiens* in the larger dimensions of the malleus and incus, the smaller size and asymmetry of the stapes, the more open angle of the malleus and a more closed

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[1] Heim (1982) also mentions the presence of an incus within the tympanic cavity in La Ferrassie 4 bis. This specimen was said to closely resemble the incus in the LF3 individual. However, examination of the original specimen did not reveal the presence of an incus, nor is a photo of the specimen included in the monograph on the La Ferrassie children. Thus, the existence of this specimen is currently known only from the reference to it by Heim.

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angle of the incus (Heim, 1982). Nevertheless, Heim was appropriately cautious in interpreting whether these slight differences held any evolutionary significance or were merely the result of individual variation.

Several more recent studies have provided additional data for the LF3 ossicles (Masali et al., 1991; Spoor, 2002; Crevecoeur, 2007; Quam and Rak, 2008), based largely on measurements obtained from the scaled photo published by Heim. Since the original specimens were previously unavailable for study, this represented the only approach possible to obtain further metric data on these specimens. However, given the quality of the photograph, the imprecise orientation and very small size of the ossicles, this data should be considered tentative. On a recent trip, one of us (RMQ) was able to study the original fossil specimens.

Several developments since the original publication make a reassessment of the LF3 ear ossicles warranted. Studies of the inner ear in Neandertals have revealed differences from *H. sapiens* in several aspects (Spoor et al., 2003), and despite their diminutive size, the middle ear ossicles are particularly well-suited to drawing phylogenetic inferences. At birth, these tiny bones are fully formed and have already reached adult dimensions (Scheuer and Black, 2000). The embryological origin of each of the ear bones has been thoroughly studied, and their development is under tight genetic control (Mallo, 1998, 2001; Frenz et al., 2001). Comparative genomic studies have revealed accelerated rates of evolution in several genes related to hearing in humans compared with chimpanzees (Clark et al., 2003), including some (e.g., Eya1) that may be directly related to the formation of the ossicles (Xu et al., 1999). A standardized measurement protocol, relying in part on previous studies (Masali, 1964), has been developed for the auditory ossicles (Quam and Rak, 2008), and the fossil sample of these tiny bones has been augmented considerably (Arensburg et al., 1996; Tillier, 1999; Maureille, 2002; Spoor, 2002; Lisonek and Trinkaus, 2006; Quam et al., 2006; Crevecoeur, 2007). In addition, the ear ossicles play an important physiological role in audition (Wever and Lawrence, 1954; Kirikae, 1960). Anatomical differences in the ear ossicles across primates have been shown to be correlated with aspects of their hearing sensitivity (Coleman and Ross, 2004; Coleman and Colbert, 2010), and fossil hominin ear ossicles have been included in models that reconstruct the auditory capacities in hominin species (Martínez et al., 2004, in press; Quam et al., 2012).

The preservation of a complete ossicular chain in LF3 is exceptional. The only other published fossil hominin specimens to preserve all three ear ossicles are the Middle Paleolithic *H. sapiens* specimen from Darra-i-Kur (Angel, 1972) and the recently rediscovered Le Moustier 2 Neandertal infant (Maureille, 2002). In addition to LF3, published data on Neandertal ear ossicles is mainly limited to the stapes from Subalyuk 2 and the incudi from Amud 7 and Le Moustier 1 (Arensburg et al., 1996; Ponce de León and Zollikofer, 1999; Quam and Rak, 2008). The study of the ear ossicles in LF3, then, provides an opportunity to confirm the limited observations made on these isolated specimens and promises to reveal new insights into the evolution of the auditory apparatus in Neandertals.

Materials and methods

The La Ferrassie 3 ear ossicles

The three ear ossicles were recovered from the right tympanic cavity. Since the original publication, the LF3 ear ossicles have suffered some damage, which limits the information that can be obtained. The malleus appears to be complete, but is broken in two pieces, corresponding to the manubrium and the head/neck (Fig. 1). These have been glued together in the past, although they are currently not in their proper anatomical position. In particular, the head/neck is glued to the superior border of the lateral process, rather than joining with the manubrium laterally. This has the effect of artificially elongating the specimen and the typical angulation between the head and the manubrium is not accurately represented. Close comparison of the present-day specimen with the photograph published by Heim (1982) indicates that the specimen was already in its present state at the time of its publication. This means that the metric dimensions published previously by Heim and others need to be revised. Examination under a standard light microscope reveals that both the tip of the manubrium and the lateral process are complete and undamaged. However, the top of the head shows some erosion of the surface bone near the margin of the articular facet. The incorrect orientation of the two main pieces and the thick coating of adhesive prevent observation of a few anatomical features.

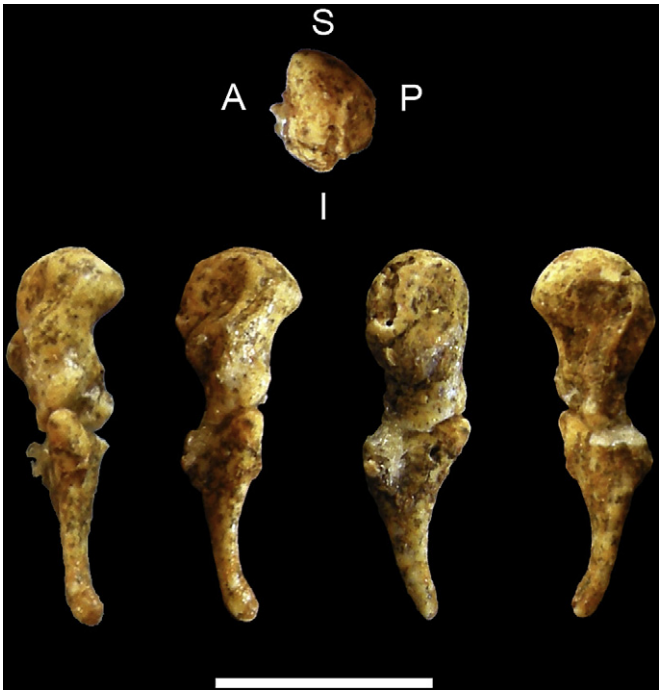

Figure 1. The LF3 malleus. The bone appears to be complete, but the two major fragments are incorrectly aligned, prohibiting a standard view of the bone. The view on the far left corresponds approximately to the view published by Heim (1982). The other three views show slightly different orientations of the bone. Note the curvature of the lateral surface of the manubrium. Scale bar = 5 mm.

Although the true maximum length cannot currently be determined, the maximum length of the bone as it is presently (incorrectly) reconstructed was measured in several slightly different orientations of the bone (Fig. 1), including the view that appears to correspond to that published by Heim. The highest value obtained in any of these views was 8.74 mm (8.54–8.74 mm range). This value is larger than that reported by Heim (8.3 mm), but shorter than that measured by Spoor (2002) (9.0 mm) and Crevecoeur (2007) (8.9 mm) on the published photograph. Although all of these estimates are unreliable since they were taken on the incorrectly reconstructed malleus, the true maximum length is unlikely to be as long as 9.0 mm, as suggested by Spoor (2002).

Given the preservation conditions, every attempt was made to measure as many standard dimensions as possible, paying close attention to preservation of the bone and identification of reliable anatomical landmarks. Despite these preservation issues, measurements of the manubrium and head/neck in the present study