

Jacopo Moggi-Cecchi

Laboratori di Antropologia, Dipartimento di Biologia Animale e Genetica, Università di Firenze, via del Proconsolo, 12, Florence 50122, Italy.

Palaeoanthropology Unit for Research and Exploration, and Sterkfontein Research Unit, University of the Witwatersrand, Johannesburg, South Africa.  
E-mail: jacopo@unifi.it

Mark Collard

Department of Anthropology, and AHRB Centre for the Evolutionary Analysis of Cultural Behaviour, University College London, Gower Street, London WC1E 6BT, U.K.  
E-mail: m.collard@ucl.ac.uk

*Keywords:* Stapes, hominid, Sterkfontein, *Australopithecus*, *Homo habilis*, hearing.

*Journal of Human Evolution* (2002) 42, 259–265  
doi:10.1006/jhev.2001.0524

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### Introduction

The three small bones of the human middle ear—the malleus, incus and stapes—have been the subject of research since the mid fifteenth century (Arensburg *et al.*, 1981). Consequently, knowledge of their anatomy and embryology is extensive (e.g. Schuknecht & Gulya, 1986; McPhee & Van de Water, 1988). Middle ear bones have also been well studied in other extant primates and in Neanderthals (e.g., Masali & Chiarelli, 1965*a,b*; Masali, 1968; Arensburg & Nathan, 1972; Hershkovitz, 1977; Heim, 1982; Arensburg & Tillier, 1983; MacPhee & Cartmill, 1986; Masali *et al.*, 1991; Arensburg *et al.*, 1996). However, relatively little is known about the middle ear bones of early hominids. Hitherto, the only Plio-Pleistocene hominid ear ossicle described is an incomplete incus recovered from the temporal bone of a specimen assigned to *Australopithecus robustus* (SK 848) from Swartkrans, South Africa (Rak & Clarke, 1979*a,b*; Rak, 1994). In this paper, we describe a second early hominid middle ear bone, a stapes, which was recently found in association with a specimen from Sterkfontein, South Africa. We also outline

a functional analysis that was prompted by the discovery of the ossicle, and which has implications for the hearing capabilities of early hominids.

### Discovery and morphological description

The fossil stapes was recovered by one of us (J.M.-C.) while cleaning the exposed middle ear cavity of the left petrous bone of Stw 151, the partial cranium of a juvenile early hominid excavated from Member 4 of Sterkfontein, South Africa (Moggi-Cecchi *et al.*, 1998). Stw 151 was originally assigned to *Australopithecus africanus* (Tobias, 1983), although this attribution has recently been questioned (Moggi-Cecchi *et al.*, 1998). The stapes was located in the vestibule of the inner ear, presumably having slipped through the oval window before fossilization. As can be seen in Figure 1, a large crystal of calcite occupies the central portion of the superior edge of the footplate. To avoid damaging the specimen, no attempt has been made to remove the crystal.

The shape of the Stw 151 stapes is subtriangular, with the anterior crus, posterior



Figure 1. Superior view of left stapes of Stw 151. Scale=1 mm.

crus and footplate having approximately equal lengths. The neck is very short and ill defined. The head is also short, oval in lateral outline, with a marked lenticular process of the incus facing laterally. Posterior to the head, a deep, concave and oval insertion facet for the stapedius muscle is evident. The footplate is thin mediolaterally, with flanged anterior and posterior edges.

### Comparative metrical analysis

The completeness of the Stw 151 stapes allows a number of measurements to be taken. The maximum height of the stapes and the length of its footplate are reported in Table 1, along with comparable data for several modern human populations that were taken from the literature. All of the values recorded for the Stw 151 stapes fall outside the ranges of variation in the human samples. Since the ear ossicles of extant mammals attain their adult size by the fifth month of development (McPhee & Van de Water, 1988; Masali *et al.*, 1992), it is unlikely that the small size of the fossil stapes is due to the young age of the

specimen with which it is associated. It is also worth noting that while the stapes shows marked variability in *Homo sapiens* (Heron, 1923; Masali, 1964; Sarrat *et al.*, 1988), it is the least variable of the three ossicles (Masali, 1968; Masali *et al.*, 1992).

Table 2 reports the area of the footplate of the Stw 151 stapes together with comparable data from the La Ferrassie III Neanderthal specimen, modern humans, chimpanzees, gorillas and orang-utans. Despite the small samples sizes, these data show that great apes have smaller stapedia footplates than humans, and that the ranges of variation for humans and great apes do not overlap. The data also show that Stw 151 stapedia footplate area falls well within the great ape range of variation, and that the La Ferrassie III stapes is within the modern human size range. A broad, positive correlation exists between the footplate area and body weight in extant mammals (Rosowski & Graybeal, 1991). However, the relationship does not seem to hold among the taxa in our comparative dataset, since the mean area of the footplate in modern humans (males ca. 60 kg, females ca. 50 kg) and chimpanzees (males ca. 50 kg, females ca. 40 kg) is greater than in gorillas (males ca. 170 kg, females ca. 80 kg) and orang-utans (males ca. 80 kg, females ca. 35 kg) (Smith & Jungers, 1997). This suggests that the size of the footplate of the Stw 151 stapes is not simply a function of the small size of the individual from which it is derived.

As no other early hominid stapes are available for comparison, we measured the area of the oval window in five specimens from Sterkfontein (including Stw 151) where the petrous bone is preserved, and where all or part of the external acoustic meatus is broken, thereby exposing the middle ear structures. Since the footplate of the stapes inserts into the oval window, the size of the oval window is a reasonable proxy for the area of the footplate. The areas were

**Table 1** Measurements of Stw 151 and modern human stapes

Stw 151	Stapes maximum height (mm)				Footplate length (mm)			
	2.42				2.46			
	<i>n</i>	<i>x</i>	Range	S.D.	<i>n</i>	<i>x</i>	Range	S.D.
<i>H. sapiens</i> (1)	—	3.26	2.56–3.78	—	—	2.99	2.64–3.36	—
<i>H. sapiens</i> (2)	—	—	—	—	19	3.40	3.00–4.40	—
<i>H. sapiens</i> (3)								
Natufian	3	3.30	3.08–3.57	0.25	4	2.90	2.81–3.03	0.10
Roman	13	3.30	3.06–3.59	0.14	13	2.80	2.57–3.09	0.12
Recent Indian	19	3.20	2.89–3.72	0.21	18	2.80	2.49–3.05	0.15

The linear measurements were taken on microphotographs at  $20\times$  with a digital caliper with a 0.01 mm accuracy, using the methods and the reference points suggested by other authors (Arensburg & Nathan, 1972; Masali *et al.*, 1992; Ehtler *et al.*, (1994). *H. sapiens* (1)=Schuknecht & Gulya (1986). *H. sapiens* (2)=Heron (1923). *H. sapiens* (3)=Arensburg *et al.* (1981).

**Table 2** Stapedial footplate area in Stw 151, the La Ferrassie III Neanderthal specimen and extant hominoids

Stw 151	Stapedial footplate area (mm <sup>2</sup> )			
	2.12			
	<i>n</i>	<i>x</i>	Range	S.D.
La Ferrassie III		3.30		
Modern humans	4	3.22	2.80–3.50	0.27
Chimpanzees	7	2.44	2.30–2.60	0.11
Gorillas	5	2.24	2.10–2.40	0.10
Orang-utans	5	1.93	1.50–2.50	0.47

Stw 151 measured following Masali *et al.* (1991). La Ferrassie III and hominoid data from Masali *et al.* (1991, 1992).

obtained digitally from photographs of the oval windows taken at  $10\times$  (Masali *et al.*, 1991). Four of the specimens measured—Stw 98, 151, 259 and 329—are currently considered to be *A. africanus*. The fifth specimen, Stw 53, has been assigned to *H. habilis* (Clarke, 1985; Tobias, 1991; but see Grine *et al.*, 1996).

The fossil hominid oval window areas are presented in Table 3. The values range from 1.82 to 2.68 mm<sup>2</sup>, with a mean value of 2.33 mm<sup>2</sup>. The oval window area of

**Table 3** Fossil hominid oval window areas

Specimen	mm <sup>2</sup>
Stw 53	2.18
Stw 151	2.29
Stw 98	2.67
Stw 259	2.68
Stw 329	1.82
Mean	2.33

Microphotographs at  $10\times$  of the oval windows were taken, and their areas measured using a digitizer, following Masali *et al.* (1991).

Stw 151 is 2.29 mm<sup>2</sup>, which is consistent with a footplate area of 2.12 mm<sup>2</sup>. When compared with data on stapes footplate areas of hominoids (Table 2), the fossil hominid oval window areas overlap with the footplate areas for the great apes and fall outside the range of distribution of footplate areas for modern humans. The latter finding is striking given that the area of the oval windows is necessarily larger than the area of the footplate. Thus, the data presented in Table 3 indicate a marked difference in stapedial footplate size between *Australopithecus* and living great apes on the one hand, and modern

humans on the other. The data also suggest that the footplate size of *Homo habilis* specimen Stw 53 is more similar to those of *A. africanus* and the living great apes than it is to those of modern humans.

### Implications for early hominid hearing

The mammalian middle ear ossicular chain, which is formed by the malleus, incus and stapes, conducts sound vibrations from the tympanic membrane to the fluid-filled cochlea (Dallos, 1973). The vibrations are transformed in the cochlea into electrical activity that is transmitted to the auditory tracts of the brain stem and the auditory receptive fields of the cerebral cortex (Durrant & Lovrinic, 1977). Thus, the stapes plays a crucial role in the hearing system of mammals and there is reason to think that stapes size and shape may be informative regarding the hearing capabilities of early hominids.

Attempts to use the middle ear structures of fossil taxa to make inferences about their hearing have employed two different approaches. A biomechanical approach has been applied to functional features of the Neanderthal hearing system (Masali *et al.*, 1991). This is based on a model in which the middle ear structures are assumed to act as a perfect acoustic transformer that transmits all the energy it gathers to the cochlea. The amount of sound energy transmitted from the external to the inner ear is then estimated on the basis of the lever arms of the incus and malleus, and the surface areas of the tympanic membrane and the stapes footplate. However, it has been shown (Rosowski & Graybeal, 1991; Rosowski, 1992) that the assumption that the middle ear structures act as a perfect acoustic transformer is questionable. This is because the structures of the middle ear, including the ossicles and their attachments as well as the tympanic membrane, absorb much of the acoustic energy that enters the

middle ear. Furthermore, application of this approach requires specimens preserving the entire chain of ossicles and the complete area of attachment for the tympanic membrane. At present, no early hominid specimen preserves all these parts of the hearing system simultaneously, making the application of the approach unfeasible.

The second approach to inferring hearing capabilities of fossil taxa from their middle ear structures is based on a reported allometric relationship between the sizes of auditory structures (area of the tympanic membrane, footplate area, length of the basilar membrane) and hearing capabilities in living mammals (Rosowski & Graybeal, 1991; Rosowski, 1992). Footplate area in mammals has been found to be correlated with the range of audible frequencies, so that taxa with large footplate areas are usually better at detecting low-frequency sounds, while those with small footplate areas are generally better at perceiving high-frequency sounds (Rosowski & Graybeal, 1991; Rosowski, 1992). This approach has been applied to predict features of the hearing mechanism of the early mammal *Morganucodon* (Rosowski & Graybeal, 1991).

All nonhuman primate species that have been examined in auditory threshold studies have been found to have an enhanced sensitivity to high-frequency sounds compared to modern humans (Elder, 1935; Masterton *et al.*, 1968; Stebbins, 1973; Beecher, 1974; Kojima, 1990; Stebbins & Moody, 1994; Jackson *et al.*, 1999). Although this difference is not especially marked in the context of mammal auditory threshold variation (Jackson *et al.*, 1999), it nonetheless has interesting implications for early hominid hearing. Given the aforementioned relationship between footplate area and frequency perception, it implies that *A. africanus* and *H. habilis*, which have stapedial footplate areas in the great ape size range, would also have had a greater sensitivity

to high-frequency sounds than modern humans. It is possible that the putative difference between the hearing capabilities of early hominids and modern humans is the result of natural selection. However, it is also possible that the hearing capability difference is a consequence of the difference in head size between early hominids and modern humans, since mammalian stapes size has been found to correlate with interaural width, as well as with frequency perception (Heffner, 1997).

Additional data on the morphology of the auditory structures of living and fossil hominids derive from a study of the bony labyrinth (Spoor, 1993). Among other variables, the height and the width of the basal coil of the cochlea were measured using CT imaging techniques. This study showed that cochlear size (which is related to length of the basilar membrane, one of the structures responsible for the mechanism of hearing) is larger in humans than in great apes. The seven fossil hominid specimens from Sterkfontein (including Stw 151) that were examined by Spoor (1993) all yielded values closer to those for chimpanzees than modern humans, Stw 151 being significantly smaller than modern humans (Spoor, 1993). In extant mammals there appears to be a relationship between length of the basilar membrane of the cochlea and frequency perception (Rosowski & Graybeal, 1991; Echterler *et al.*, 1994), although those conclusions have been disputed (Spoor & Zonneveld, 1998). For generalized species (that is excluding mammals with a specialized cochlea, such as bats, mole rats, dolphins, etc.) as basilar membrane length decreases, the range of hearing limits shifts to higher frequencies (Echterler *et al.*, 1994). The existence of a smaller cochlea, and thus of a shorter basilar membrane, in the fossil hominids from Sterkfontein, may thus also indicate that they had an enhanced ability to detect higher frequencies compared to modern humans.

## Conclusions

The analysis of the fossil stapes of the specimen Stw 151, together with that of the middle ear structures of other fossil specimens from Sterkfontein and extant hominids, has provided new information on the anatomy of this area, which hitherto has been poorly known in early hominids. It has also provided indications about the possible hearing capabilities of early hominids, which may have been more sensitive to high-frequency sounds than modern humans. Lastly, because of the similarities between the early hominids and living great apes in stapodial morphology, it adds a potential symplesiomorphy to the list that are known to characterize the species *A. africanus* (Tobias, 1998) and *H. habilis* (Wood & Collard, 1999).

## Acknowledgements

We thank L. Berger, P. V. Tobias and B. Kramer for permission to study the fossils. We are also grateful to L. C. Aiello, J. Allan, M. Cartmill, M. Clegg, M. C. Dean, H. Jerison, W. H. Kimbel, M. Lake, D. Lieberman, C. Lockwood, J. Masters, J. Ohman, J. J. Rosowski, S. Shennan, F. Spoor, W. Stebbins, J. Stewart, I. Tattersall, P. V. Tobias and B. A. Wood for commenting on earlier versions of this paper. We are particularly indebted to D. Lieberman for highlighting the work linking stapes size with interaural width. This work was funded by the Palaeo-Anthropology Research Group, University of the Witwatersrand (J.M.-C.), and the Wellcome Trust (M.C.).

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