A fossil stapes from Sterkfontein, South Africa, and the hearing capabilities of early hominids

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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 sub-triangular, 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 pro-
cess 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 com-
parable 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 stapedial
footplates than humans, and that the ranges
of variation for humans and great apes do
not overlap. The data also show that Stw
151 stapedial 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 corre-
lation exists between the footplate area and
body weight in extant mammals (Rosowski
& Graybeal, 1991). However, the relation-
ship 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 avail-
able 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			
	n	x	Range	S.D.	*n*	x	Range	S.D.
H. sapiens (1)	—	3·26	2·56–3·78	—	—	2·99	2·64–3·36	—
H. sapiens (2)	—	—	—	—	19	3·40	3·00–4·40	—
H. sapiens (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 × 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; Echtler *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 (mm²)			
	2·12			
	n	x	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).

Table 3 Fossil hominid oval window areas

Specimen	mm²
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 × of the oval windows were taken, and their areas measured using a digitizer, following Masali *et al.* (1991).

obtained digitally from photographs of the oval windows taken at 10 × (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 mm², with a mean value of 2·33 mm². The oval window area of

Stw 151 is 2·29 mm², which is consistent with a footplate area of 2·12 mm². 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 sug-
gest that the footplate size of *Homo habilis*
specimen Stw 53 is more similar to thoseof
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 trans-
mits 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 mem-
brane. 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 allo-
metric 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 sensi-
tivity 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 differ-
ence 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 relation-
ship between footplate area and frequency
perception, it implies that *A. africanus* and
H. habilis, which have stapedial foot-
plate 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; Echteler *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 (Echteler *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 hominoids, 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 stapedial 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

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