

# The inner ear of the *Paranthropus* specimen DNH 22 from Drimolen, South Africa

Amélie Beaudet<sup>1,2,\*</sup>

<sup>1</sup>School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Johannesburg, South Africa

<sup>2</sup>Department of Anatomy, University of Pretoria, Pretoria, South Africa

\*Correspondence

Amélie Beaudet, School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Private Bag 3, Johannesburg, WITS 2050, South Africa.

Email: beaudet.amelie@gmail.com

## Abstract

### *Objectives*

Morphological variation within the southern African hypodigm of *Paranthropus* has been the focus of major interest since the earliest discoveries in the “Cradle of Humankind.” Given the relevance of the bony labyrinth for investigating fossil primate paleobiodiversity, this article aims to provide additional evidence for assessing the degree of regional variation within *Paranthropus* through the comparative analysis of the inner ear of DNH 22.

### *Materials and methods*

As comparative material, 18 southern African hominin specimens from Sterkfontein, Swartkrans, and Makapansgat (plus published data from Kromdraai B), attributed to *Australopithecus*, early *Homo* or *Paranthropus*, as well as 10 extant human and 10 extant common chimpanzee specimens are investigated. A landmark-based geometric morphometric method is applied for quantitatively assessing labyrinthine morphology. Additionally, cochlear parameters and oval window area are measured.

### *Results*

In terms of semicircular canal and cochlear shape, DNH 22 most resembles the *Paranthropus* specimen SKW 18 from Swartkrans. Both specimens differ from the other *Paranthropus* specimens investigated in this study by an anteroposteriorly large posterior semicircular canal and a cochlea with loose turns in the apical portion. Conversely, the oval window area in DNH 22 closely fits the range observed in *Paranthropus* from Swartkrans and Kromdraai B.

### *Discussion*

The inner ear of the DNH 22 specimen represents a unique opportunity to provide further insight into the early hominin labyrinthine variation pattern. In particular, the description of DNH 22 raises critical questions on the diversity of the vestibular system and evolutionary pattern of the auditory apparatus in *Paranthropus*.

**KEYWORDS:** cochlea, Cradle of Humankind, early hominins, Plio–Pleistocene, semicircular canals

## 1 INTRODUCTION

Morphological variation within the southern African hypodigm of *Paranthropus* has been the focus of major interest since the earliest discoveries at Kromdraai B and Swartkrans, both located in the “Cradle of Humankind” (CoH) (Broom, 1938, 1949). In particular, Broom (1949) initially suggested a species level distinction based on morphological and metrical differences in the dentition between the Kromdraai B assemblage, referred to *Paranthropus robustus*, and the Swartkrans assemblage, attributed to *Paranthropus crassidens*. However, even if some later studies concurred with the existence of multiple *Paranthropus* species in southern Africa (e.g., Grine, 1982, 1985; Howell, 1978), revisions of the fossil record as well as recent discoveries in the CoH converge toward a single, variable species (i.e., *P. robustus*) (e.g., de Ruiter et al., 2009; Grine, Jacobs, Reed, & Plavcan, 2012; Keyser, 2000; Menter, Kuykendall, Keyser, & Conroy, 1999; Moggi-Cecchi, Menter, Boccone, & Keyser, 2010; Steininger, Berger & Kuhn, 2008). Besides regional variation, temporal depth might represent an additional confounding factor for interpreting taxonomic diversity, as demonstrated by the diachronic changes reported in the *Paranthropus* assemblage from Kromdraai B (Braga et al., 2013, 2017).

Morphology of the bony labyrinth is particularly relevant for investigating fossil primate paleobiodiversity (e.g., Beaudet et al., 2016, 2019; Braga et al., 2013; Rook et al., 2004; Spoor, 1993). Recent assessment of the 3D variation pattern in labyrinthine morphology in southern African hominins, including *Australopithecus* from Sterkfontein and Makapansgat, and *Paranthropus* and *Homo* from Swartkrans, has revealed a specific configuration of the posterior canal in the *Paranthropus* specimens SK 46 and SK 47 that differs from the rest of the fossil hominin taxa investigated, including the other *Paranthropus* specimen SKW 18 (Beaudet et al., 2019). Moreover, the latter shows intriguing early *Homo*-like cochlear morphology and proportions that are not shared with the former two. However, as this study was limited to a few *Paranthropus* specimens, all coming from the site of Swartkrans, implications of these results for understanding the degree of morphological variation in the *P. robustus* hypodigm were limited.

Besides Swartkrans and Kromdraai B, Drimolen has played a significant role in the discussion of southern African *Paranthropus* diversity (Keyser, 2000; Moggi-Cecchi et al., 2010). With over 80 fossil hominin specimens attributed either to *P. robustus* or to *Homo* sp., the Drimolen hominin assemblage represents the second largest sample of *P. robustus* after Swartkrans (Moggi-Cecchi et al., 2010). Among the hominin remains published in 2000, the subadult specimen DNH 22 preserves the right petrous part of the temporal bone containing a complete bony labyrinth (Keyser, Menter, Moggi-Cecchi, Pickering, & Berger, 2000; Moggi-Cecchi et al., 2010; this study). The temporal bone, associated with cranio-dental material, has been attributed to *P. robustus* (Keyser et al., 2000; Moggi-Cecchi et al., 2010). This specimen therefore represents a unique opportunity to investigate further the variation pattern of the inner ear in fossil *Paranthropus*.

Through the comparative analysis of the inner ear of DNH 22, this article thus aims to provide additional evidence for assessing the degree of regional variation within the southern African *Paranthropus* hypodigm.

## 2 MATERIALS AND METHODS

Information on comparative fossil and extant specimens is summarized in Table 1 (more details could be found in Beaudet et al., 2019). Data from Kromdraai B have been reported from Braga et al. (2013, 2015, 2017). *Australopithecus* specimens ( $n = 11$ ) are from Sterkfontein (Member 2, Member 4, and Jacovec Cavern) and Makapansgat (Member 4) deposits ranging from 4.02 (or at least 3.67) and 2.01 million years (Ma) old (Granger et al., 2015; McKee, Thackeray, & Berger, 1995; Partridge, Granger, Caffee, & Clarke, 2003; Pickering & Kramers, 2010). *Paranthropus* ( $n = 5$ ) and early *Homo* ( $n = 2$ ) specimens are from Swartkrans Member 1 dated to 2.19–1.80 Ma (Gibbon et al., 2014; Herries, Curnoe, & Adams, 2009; Pickering et al., 2012; Sutton et al., 2009) plus two specimens from Kromdraai B (TM 1517 and KB 6067) with an age around 2 Ma (Delson, 1988; Gilbert, Frost, & Delson, 2016; Heaton, 2006; McKee et al., 1995; Thackeray & Gommery, 2002; Vrba, 1981) for which the measurements have been reported from Braga et al. (2013, 2015, 2017). Macromammalian assemblage from Drimolen indicates an age of ca. 2.0 to ca. 1.5 million years based on correlations with Member 1 of Swartkrans (Gibbon et al., 2014; Keyser, 2000; Keyser et al., 2000). More recently, U–Pb dating methods applied on top, middle, and basal flowstones at Drimolen revealed an age of 2.67–1.79 Ma (Pickering et al., 2019). All *Australopithecus*, *Paranthropus* and early *Homo* specimens are housed in the Ditsong National Museum of Natural History in Pretoria and the Evolutionary Studies Institute at the University of the Witwatersrand in Johannesburg (South Africa; Table 1).

Our comparative sample of extant specimens comprises adult humans (*Homo sapiens*,  $n = 10$ ) and common chimpanzees (*Pan troglodytes*,  $n = 10$ ) with equal proportions of males and females within each taxon. Extant humans and chimpanzees are curated in the Pretoria Bone Collection (L'Abbé, Loots, & Meiring, 2005) at the University of Pretoria (South Africa) and in the Royal Museum for Central Africa in Tervuren (Belgium), respectively (Table 1).

The DNH 22 temporal bone was scanned at the microfocus X-ray tomography facility of the Palaeosciences Centre at the University of the Witwatersrand, in Johannesburg (South Africa), at a spatial resolution of 26.7  $\mu\text{m}$  (isotropic voxel size). With the exception of the two specimens from Kromdraai B for which data were reported from previous publications, all comparative specimens investigated in this study were similarly imaged by microfocus X-ray tomography using various systems (Table 1).

Labyrinthine surfaces from Sterkfontein, Makapansgat, and Swartkrans were obtained using Avizo v9.0 software (Visualization Sciences Group, Inc., Berlin, Germany) combining the region-based segmentation approach that relies on topographic concepts and which is known as the “watershed transform” (Roerdink & Meijster, 2001) and manual corrections. The morphology of the inner ear was investigated through a semilandmark-based three-dimensional geometric morphometric approach on the outer surface following the protocol detailed in Beaudet et al. (2019). Conformations of the inner ear were comparatively assessed through a generalized Procrustes analysis (Bookstein, 1991) and the package Geomorph (Adams, Collyer, Kaliontzopoulou, & Sherratt, 2017) for R v.3.2.1 (Development Core Team, 2015). Shape variation in the comparative sample was examined through a principal component analysis and DNH 22 was subsequently projected onto the resulting principal component axes (Dryden & Mardia, 2016). The semicircular canals were investigated separately from the cochlea. Because data from Kromdraai B have been reported from previous publications and therefore limited to the cochlear parameters, the 3D shape of the

inner ear as described by landmark-based morphometric analyses of TM 1517 and KB 6067 has not been investigated in this study (Table 1).

**TABLE 1** Comparative sample used for analyzing and comparing inner ear morphology

Specimens/samples	Site/provenance	Stored at	Imaging facility	Voxel size ( $\mu\text{m}$ ) <sup>a</sup>	GM SCC	GM cochlea	Cochlear parameters	OWA
Fossil specimens/samples								
<i>Australopithecus</i>								
Sts 5	Sterkfontein Member 4	DNMNH	Pal. Centre	75.0	X	X	X	-
Sts 19	Sterkfontein Member 4	DNMNH	Necsa	44.3	X	X	X	-
StW 53 g	Sterkfontein Member 4/5 <sup>b</sup>	ESI	Pal. Centre	24.6	X	X	X	X <sup>c</sup>
StW 98	Sterkfontein Member 4	ESI	Pal. Centre	33.1	X	X	X	X <sup>c</sup>
StW 151c	Sterkfontein Member 4/5 <sup>b</sup>	ESI	Pal. Centre	28.3	X	X	X	X <sup>c</sup>
StW 255	Sterkfontein Member 4	ESI	Pal. Centre	33.1	X	X	X	X <sup>c</sup>
StW 329	Sterkfontein Member 4	ESI	Pal. Centre	33.1	X	X	X	X <sup>c</sup>
StW 498o	Sterkfontein Member 4	ESI	Pal. Centre	28.1	X	X	X	X <sup>c</sup>
StW 573	Sterkfontein Member 2	ESI	Pal. Centre	88.0	X	X	X	-
StW 578	Jacovec Cavern	ESI	Pal. Centre	66.6	X	X	X	-
MLD 37/38	Makapansgat Member 4	ESI	Pal. Centre	80.8	X	X	X	-
<i>Paranthropus</i>								
SK 46	Swartkrans Member 1	DNMNH	Pal. Centre	72.6	X	X	X	-
SK 47	Swartkrans Member 1	DNMNH	Pal. Centre	71.2	X	-	-	-
SK 1585	Swartkrans Member 1	DNMNH	Necsa	45.9	-	X	X	-
SK 879	Swartkrans Member 1	DNMNH	Max Planck	13.5	-	X	X	X <sup>c</sup>
SKW 18	Swartkrans Member 1	DNMNH	Max Planck	36.4	X	X	X	X <sup>c</sup>
TM 1517	Kromdraai Member 4	DNMNH	-	-	-	-	X <sup>d</sup>	-
KB 6067	Kromdraai Member 3	DNMNH	-	-	-	-	X <sup>e</sup>	X <sup>c</sup>
Early <i>Homo</i>								
SK 27	Swartkrans Member 1	DNMNH	Necsa	80.1	X	X	X	-
SK 847	Swartkrans Member 1	DNMNH	Max Planck	63.6	X	X	X	X <sup>c</sup>
Extant specimens/samples								
Humans (n = 10)	South Africa	PBC	Necsa	98.6–114.1	X	X	X	X
Chimpanzees (n = 10)	Cameroon, Congo, Gabon, Liberia, Tanzania	RMCA	UGCT	70.0–85.0	X	X	X	X

Abbreviations: DNMNH = Ditsong National Museum of Natural History, Pretoria; ESI = Evolutionary Studies Institute; GM = geometric morphometric; Max Planck = Max Planck Society, Department of Human Evolution, Virtual Reality Laboratory, Germany; Necsa = South African Nuclear Energy Corporation SOC Ltd., Pretoria (Hoffman & de Beer, 2012); OWA = oval window area; Pal. Centre = Palaeosciences Centre, University of the Witwatersrand, Johannesburg; PBC = Pretoria Bone Collection, University of Pretoria; RMCA = Royal Museum for Central Africa; SCC = semicircular canals; UGCT = Centre for X-ray Tomography of Ghent University, Gent (Masschaele et al., 2013).

<sup>a</sup>Isotropic voxel size.

<sup>b</sup>Stratigraphic provenience is uncertain.

<sup>c</sup>Data from Braga et al. (2017).

<sup>d</sup>Data from Braga et al. (2015).

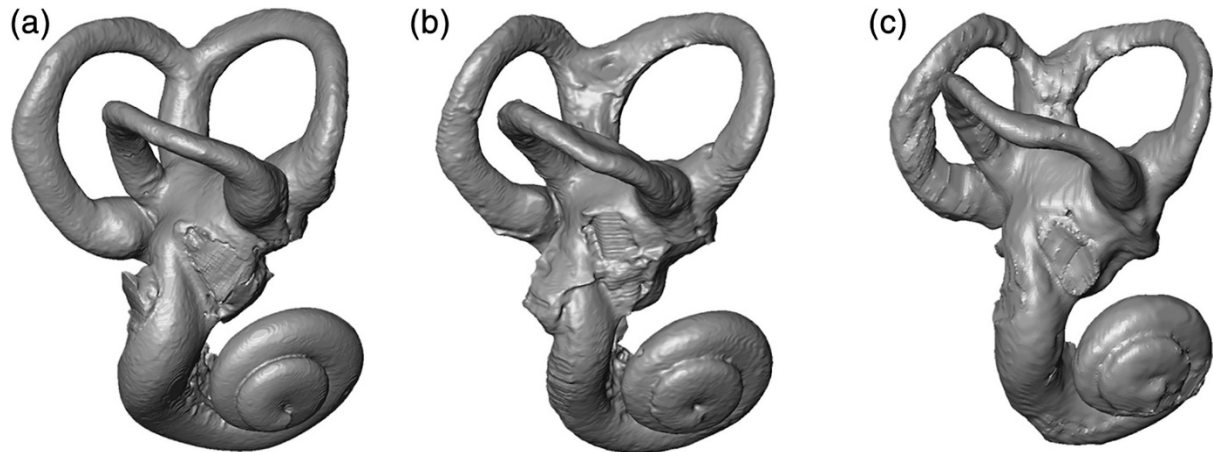
<sup>e</sup>Data from Braga et al. (2013).

Cochlear parameters (i.e., external cochlear length, number of turns, and curvature gradient) in DNH 22 were computed using MATLAB R2013a (Mathworks, <https://www.mathworks.com/products/matlab.html>) (Braga et al., 2013, 2015, 2017). Comparative data on the cochlear parameters were compiled from Braga et al. (2013, 2015) and Beaudet et al. (2019)

Finally, the oval window area (OWA) in DNH 22 and the comparative extant sample was measured following the protocol detailed in Braga et al. (2013). A section sampling the complete outline of the oval window was extracted and the OWA was segmented out by using Avizo v9.0. The area was obtained by applying the tool “Material statistics.” Comparative data for fossil specimens were compiled from Braga et al. (2017).

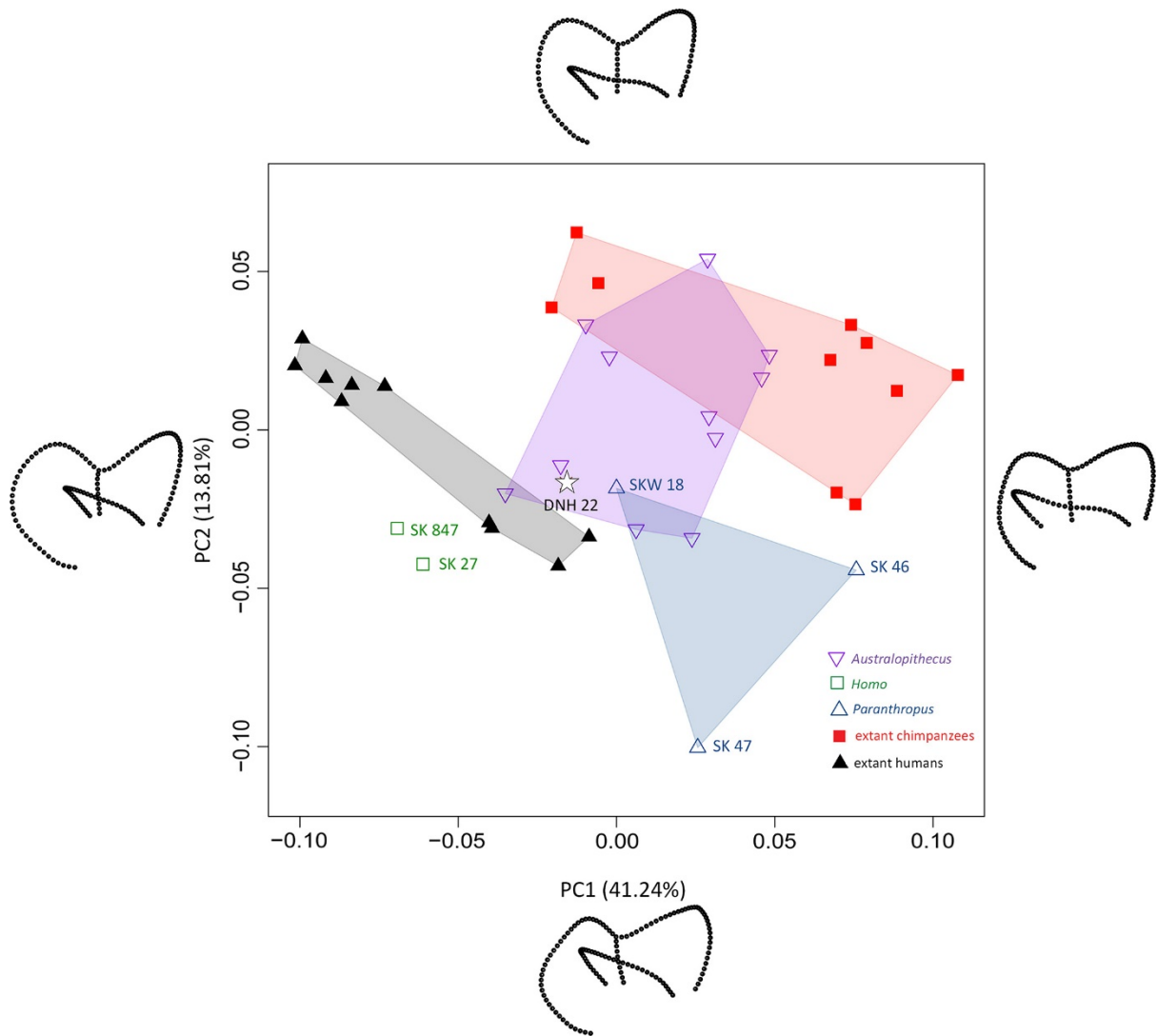
### 3 RESULTS

DNH 22 preserves the complete right bony labyrinth (Figure 1). The inner ear shape of DNH 22 is visually compared in Figure 1 with SKW 18 and SK 46, which were shown to differ substantially from each other in previous studies (Beaudet et al., 2019). The left ear of SK 46 has been mirrored. From visual inspection, DNH 22 shares with SKW 18 a short and straight lateral semicircular canal and a shorter cochlear length as compared with SK 46.

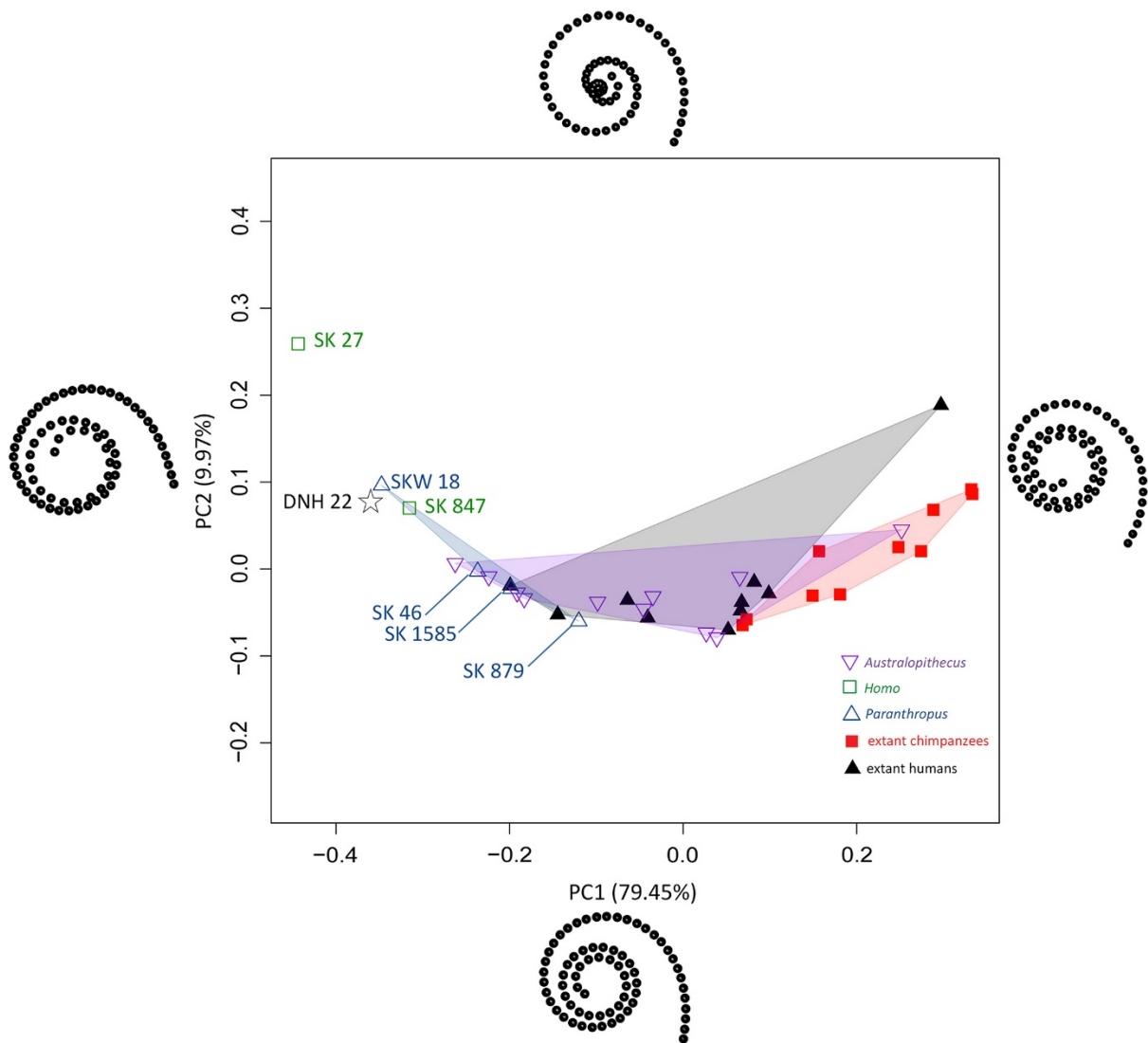


**Figure 1.** Virtual rendering of the DNH 22 inner ear (a) compared to the inner ears of the *Paranthropus* specimens SKW 18 (b) and SK 46 (c) from Swartkrans in anterolateral views. All specimens are right except SK 46 (i.e., left inner ear mirrored as right). Images not to scale

Figures 2 and 3 illustrate the principal component analyses based on Procrustes shape coordinates of the semicircular canals and the common crus, and of the cochlea, respectively. Shapes occurring at the extremes of the axes illustrate morphological trends along each component after Procrustes superimposition. In both analyses, DNH 22 more closely resembles SKW 18 than the other *Paranthropus* specimens SK 46, SK 47, SK 1585, and SK 879. In terms of semicircular canal morphology, DNH 22 and SKW 18 fall within the *Australopithecus* range and lie close to the extant human cluster along both axes, which corresponds to an anteroposteriorly large posterior semicircular canal and a mediolaterally small and straight lateral semicircular canal (Figure 2). Concerning the cochlear shape, DNH 22 and SKW 18 plot particularly close to the early *Homo* specimen SK 847 in the negative space of PC 1, which corresponds to a cochlea with loose turns in the apical portion (Figure 3). Along PC 2, they lie in between the early *Homo* specimen SK 27, which shows an extremely tight apical turn, and the rest of the fossil sample.



**Figure 2.** Principal component analysis (PCA) of the Procrustes-registered shape coordinates of the semicircular canal morphology calculated for DNH 22 and comparative Plio–Pleistocene hominins, extant humans and extant common chimpanzees and computed for PC1 and PC2. Shapes at the extremes of the axes illustrate morphological variation trends along each component



**Figure 3.** Principal component analysis (PCA) of the Procrustes-registered shape coordinates of the cochlear morphology calculated for DNH 22 and comparative Plio–Pleistocene hominins, extant humans and extant common chimpanzees and computed for PC1 and PC2. Shapes at the extremes of the axes illustrate morphological variation trends along each component

Regarding the cochlear parameters, DNH 22 falls within the variation of *Australopithecus* and *Paranthropus* in terms of external length and number of turns (Table 2; even if the external length is comparatively short in KB 6067). While the radius of the apical turn falls within the range of all of the comparative groups, the curvature gradient is closer to *Australopithecus* than to any of the other fossil groups. The value for the radius of the basal turn exceeds the variation of any of the comparative groups. As compared to extant taxa, the number of turns and the curvature gradient of the cochlea of DNH 22 are compatible with the variation of extant humans.

**TABLE 2** Cochlear parameters in DNH 22 and comparative Plio-Pleistocene hominins, extant humans and extant common chimpanzees (based on Braga et al., 2013, 2015; Beaudet et al., 2019)

Specimens/samples	ECL	TUR	R1	R2	CUR
DNH 22	34.9	2.7	1.4	4.8	3.3
<i>Australopithecus</i> (n = 11)					
Mean	35.0	2.8	1.3	3.2	2.5
Range	30.5–40.0	2.6–3.1	1.0–1.6	2.8–3.7	2.2–3.3
<i>Paranthropus</i> (n = 6) <sup>a</sup>					
Mean	35.1	2.6	1.4 <sup>b</sup>	3.3 <sup>b</sup>	2.4 <sup>c</sup>
Range	31.9–37.9	2.5–2.7	1.4–1.6 <sup>b</sup>	3.1–3.6 <sup>b</sup>	2.2–2.4 <sup>c</sup>
Early <i>Homo</i> (n = 2)					
Mean	31.1	2.4	1.5	3.0	2.0
Range	29.1–33.1	2.3–2.5	1.4–1.6	2.9–3.1	1.9–2.0
Extant humans (n = 10)					
Mean	41.0	2.8	1.5	3.7	2.6
Range	37.2–46.8	2.6–3.3	1.2–1.7	3.4–4.0	2.1–3.4
Extant chimpanzees (n = 10)					
Mean	39.2	3.0	1.3	3.2	2.6
Range	37.8–40.9	2.8–3.2	1.2–1.4	3.2–3.3	2.3–2.8

Abbreviations: CUR = gradient curvature; ECL = external cochlear length (mm); R1 = radius of the smaller last spiral turn (mm); R2 = radius of the larger first spiral turn (mm); TUR = number of turns.

<sup>a</sup>Data for TM 1517 and KB 6067 are from Braga et al. (2013, 2015).

<sup>b</sup>Data not available for TM 1517 and KB 6067.

<sup>c</sup>Data not available for KB 6067.

The OWA in DNH 22 is larger than *Australopithecus* and early *Homo* but is consistent with the variation observed in *Paranthropus* (represented by SKW 18, SK 879, KB 6067; Braga et al., 2017) and extant humans (Table 3). More particularly, the OWA in DNH 22 is similar to the specimen SKW 18 from Swartkrans (3.9 mm<sup>2</sup>; Braga et al., 2017) but larger than the specimen KB 6067 from Kromdraai (2.8 mm<sup>2</sup>; Braga et al., 2017).



**TABLE 3** Oval window area (OWA, mm<sup>2</sup>) in DNH 22 and comparative Plio–Pleistocene hominins, extant humans and extant common chimpanzees (based on Braga et al., 2017)<sup>a</sup>

Specimens/samples	OWA
DNH 22	3.9
<i>Australopithecus</i> (n = 6) <sup>a</sup>	
Mean	2.6
Range	2.0–3.4
<i>Paranthropus</i> (n = 3) <sup>a</sup>	
Mean	3.6
Range	2.8–4.1
Early <i>Homo</i> (n = 1) <sup>a</sup>	3.3
Extant humans (n = 10)	
Mean	4.1
Range	3.4–5.0
Extant chimpanzees (n = 10)	
Mean	3.2
Range	2.9–3.6

<sup>a</sup>Data from Braga et al. (2017).

## 4 DISCUSSION

The inner ear of the DNH 22 specimen represents a unique opportunity to provide further insight into the early hominin labyrinthine variation pattern. In particular, DNH 22 does not share the specific configuration of the posterior canal previously detected in the two *Paranthropus* specimens SK 46 and SK 47 (Beaudet et al., 2019; this study). On the contrary, the semicircular canal morphology in DNH 22 approximates the *Paranthropus* specimen SKW 18 and some of the *Australopithecus* specimens considered in this study. Because of the role of the semicircular canal in regulating sensory control of locomotion (rev. in Ekdale, 2016), this result might indicate a substantial variety of head movements within *Paranthropus*. However, basicranial shape differences might represent another plausible factor explaining these results (Spoor & Zonneveled, 1998). Interestingly, de Ruiter, Steininger, and Berger (2006) previously noted that the bipetrous breadth and the basioccipital length of SKW 18 are close to the values reported for *Australopithecus africanus*. Unfortunately, the DNH 22 specimen does not preserve the basicranium and potential influence of the cranium on the inner ear cannot be further tested.

DNH 22 shows the peculiar early *Homo*-like cochlear morphology described in SKW 18 (Beaudet et al., 2019; this study). The association of cranio-dental remains with the temporal bones of DNH 22 and SKW 18 prevents potential ambiguity regarding their taxonomic attribution (Clarke, 1990; de Ruiter et al., 2006; Moggi-Cecchi et al., 2010). As this trait is absent from *Australopithecus*, one may hypothesize that this feature has emerged independently in both *Paranthropus* and early *Homo*. However, the absence of such derived traits in SK 46 and SK 47 tends to reject this hypothesis and rather suggests a more complex scenario. Additionally, because the cochlear parameters indicate a mix of *Australopithecus*-like (i.e., curvature gradient) and unique (i.e., radius of the basal turn) traits in DNH 22, the description of additional specimens from Drimolen would be useful to phylogenetically

interpret this combination of features. More specifically, the very large size of the basal turn departs considerably from the range of variation of other *Paranthropus* specimens and would deserve further attention.

DNH 22 confirms the very large oval window of *Paranthropus* as compared to *Australopithecus* previously demonstrated by Braga et al. (2015). This trait, combined with the intriguing cochlear shape shared with early *Homo*, raises interesting questions regarding the functional adaptations of the hearing organ in early hominins. Unfortunately, to date, there is only one southern African early *Homo* specimen preserving both the cochlea and the oval window (i.e., SK 847), and more specimens would be needed for drawing a comprehensive evolutionary scenario of the auditory apparatus in *Paranthropus* and *Homo* (Braga et al., 2017).

Finally, the study of the Drimolen specimen is particularly useful in characterizing the diversity of the *Paranthropus* anatomy. In particular, labyrinthine traits that contribute to distinguish the inner ear of SKW 18 from the specimens SK 46 and SK 47 could no longer be considered anecdotal as they are also found in DNH 22 (Beaudet et al., 2019). This study rather confirms a certain degree of variation within the Swartkrans sample. The more recent dates of Swartkrans Member 1 suggest a temporal range of about 500,000 years for this stratigraphic unit (Gibbon et al., 2014). Accordingly, one might consider the possibility of a temporally mixed sample, with specimens representing a significant amount of evolutionary time. Under this hypothesis, SKW 18 may represent a geologically younger/older and phylogenetically more derived/primitive *Paranthropus* population as compared to SK 46 and SK 47 that could be found at the same time at Drimolen (Pickering et al., 2019). However, without a clear stratigraphic control, it is nearly impossible to evaluate potential time differences between the specimens. This possibility should be further tested in the future with additional specimens (ideally found in situ) from Swartkrans and Drimolen deposits.

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