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Morphometric comparison of semicircular canals of *Parapapio broomi* and *P. jonesi* from Sterkfontein, South Africa

As an anatomist working on modern baboons at the University of the Witwatersrand, Trevor Jones[1] described a partial cranium of a Plio-Pleistocene baboon (Sts 564) from the Sterkfontein Caves in the Cradle of Humankind. He named it *Parapapio broomi,* a new genus and species in honour of Dr Robert Broom who was based at the Transvaal Museum in Pretoria from 1934 until his death in 1951 (the museum is now referred to as the Ditsong National Museum of Natural History). Jones was a student of Professor Raymond Dart who had encouraged Broom to work at Sterkfontein after this site had yielded fossil baboons similar to those that had been found at Taung[2] – the site from which the holotype specimen of *Australopithecus africanus* was discovered in 1924[3].

It is now recognised that *Parapapio* and hominins are often found together in pene-contemporaneous Plio-Pleistocene deposits in Africa. The first hominin to be found at Sterkfontein (TM 1511, *A. africanus*) was discovered in 1936, soon after the initial discovery of fossil baboons at the site by Trevor Jones and two of Dart's other students from the University of the Witwatersrand.

Parapapio and *A. africanus* represented at Sterkfontein in a unit called Member 4 are considered to be in the order of 2.5 million years old. The earliest reported occurrence of *Parapapio* in southern Africa is based on the discovery of faunal material from Way Point 160 at Bolts Farm in the Cradle of Humankind, dated to between 4.5 and 4 million years ago.[4] As yet, no australopithecines have been found at Way Point 160, but the site has the potential to yield hominin fossils pene-contemporary with *Australopithecus anamensis* from East Africa.

Since 1936 additional primates have been found at Sterkfontein.[5-7] The oldest certain occurrences of *Parapapio* are at Sterkfontein Member 2 and Makapansgat Members 2, 3 and 4.[8] These remains are dated to between 3.5 and 2.5 Ma. Specimens formerly attributed to *Parapapio antiquus* from Taung are now considered to belong to another genus, *Procercocebus antiquus.*[9] Other discoveries of early papionins considered to represent *Parapapio* are from the 'E' Quarry (Varswater Formation) at Langebaanweg and are dated approximately at 5.1 Ma[10], and from Waypoint 160 at Bolt's Farm Cave System[4], but they are too fragmentary or rare for us to be sure of the genus to which they belong[8].

As in the case of hominin taxonomy, the classification of primates attributed to the genus *Parapapio* is fraught with problems. The taxonomy of Plio-Pleistocene *Parapapio* from South African cave sites has been revised and debated inter alia by Freedman[11,12], Freedman and Stenhouse[13], Delson[14], Eisenhart[15], Szalay and Delson[16], Jablonski[17], Heaton[18], Williams et al.[19], Fourie et al.[20], Jablonski and Frost[21], Gilbert[22] and, most recently, by Beaudet[23] and Beaudet et al.[24]; Monson et al.[25] have confirmed that the taxonomy of South African papionins is problematic.

When Jones described Sts 564 as a new genus and species in 1937, he did so with a sample of only one specimen (attributed to *P. broomi*), just as Dart[3] had done in the case of the Taung Child (*A. africanus*). With single specimens it was easy to describe new taxa. Historically, the species diversity of primates in the genus *Parapapio* increased quickly after 1937 to include *P. jonesi* (e.g. Sts 565 from Sterkfontein), *P. whitei* (e.g. Sts 563 from Sterkfontein and MP 221 from Makapansgat) in addition to *P. antiquus* (e.g. TP 8 from Taung). However, some palaeontologists such as Brain[26] have questioned the validity of several species of *Parapapio* occupying similar if not identical habitats at about the same time.

Materials

In this paper we focus our attention on two holotype specimens, not only Sts 564 (*P. broomi*) but also Sts 565 named by Broom[27] as *P. jonesi* in reciprocal honour of Trevor Jones. Both of the fossil baboon specimens come from Sterkfontein, and both are believed to be derived from the same deposit (Member 4) in which *Australopithecus africanus* is represented. The two crania are incomplete and do not have well-preserved dentition, but the semicircular canals are intact.

Method

Virtual 3D reconstruction of the semicircular canals was undertaken on the basis of micro-focus X-ray computed tomography (μXCT) scanning at the South African Nuclear Energy Corporation SOC Ltd (Necsa). Landmark coordinates were obtained after Procrustes superimposition from the two virtual semicircular canals.[23,24] A total of 100 measurements was recorded per specimen. These measurements were subjected to morphometric analyses of the kind described by Thackeray[28] in order to assess probabilities of conspecificity. Dimensions for pairs of specimens were compared using regression equations of the form $y=mx + c$ where m is the slope and c is the intercept, based on measurements of any specimen A (x-axis), and any specimen B of the same species (y-axis), and vice versa.[29]

The log-transformed standard error of the m coefficient (log se_m) is a measure of the degree of similarity between pairs of specimens, and has been shown by Thackeray and Dykes[29] (using cranial data) to have central tendency around a mean value of -1.61 ±0.10 for modern conspecific specimens. The mean log se_m value of -1.61 has been considered to be an approximation of a biological species constant, associated with a probabilistic definition of a species, applicable in modern and palaeontological contexts.[28]

The range of difference in log se_m values ('delta log se_m') is obtained from comparisons when specimen A (x-axis) is compared to B (y-axis), and secondly when specimen A (y-axis) is compared to B (x-axis). Delta log se_m is small (circa 0.03) for conspecific comparisons. A high probability of conspecificity can be expected to prevail for pairs of specimens when the mean log se_m is less than or equal to -1.61 and when delta log se_m is less than or equal to 0.03.[29]

Results

Virtual μXCT 3D images of the semicircular canals obtained from Sts 564 and Sts 565 are shown in Figure 1.

When measurements of *P. broomi* (Sts 564 on *x*-axis) are compared to those of *P. jonesi* (Sts 565 on *y*-axis), we obtain a log se_m value of -1.746. For measurements of *P. jonesi* (Sts 565 on *x*-axis) versus those of *P. broomi* (Sts 564 on *y*-axis), a log se_m of -1.714 is obtained. The delta log se_m value is 0.03. For these comparisons of the holotypes of *P. broomi* and *P. jonesi*, the mean log se_m value is -1.73.

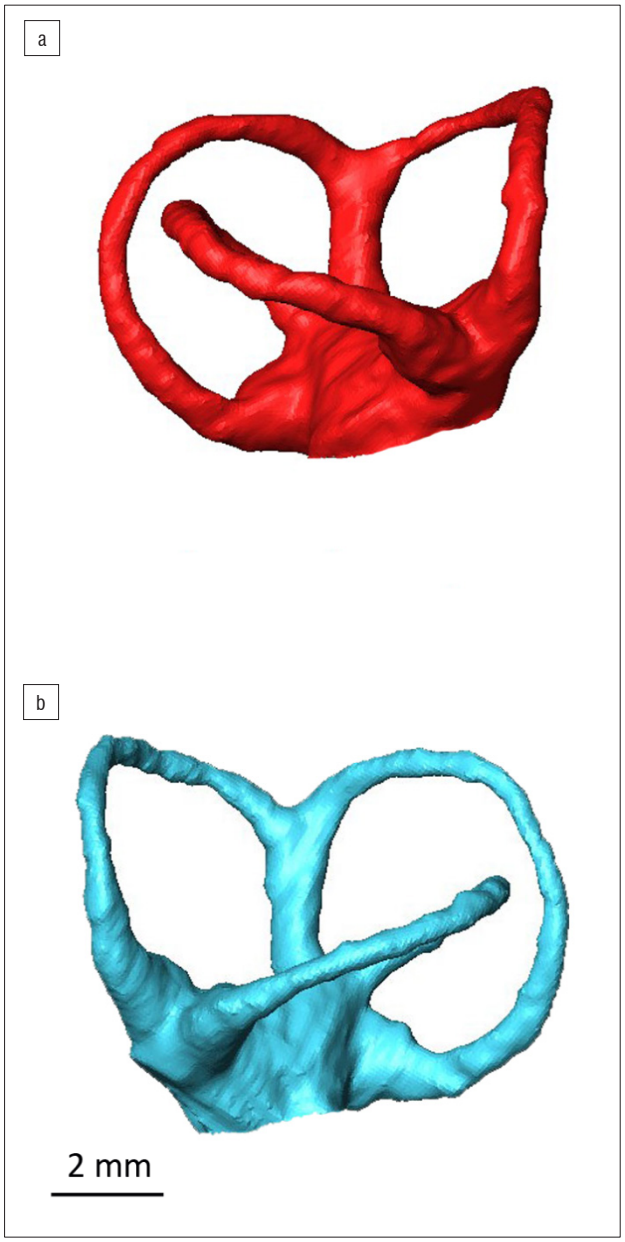

Figure 1: Virtual rendering of the semicircular canals of (a) Sts 565 and (b) Sts 564. Note differences in size but very close similarity in shape, despite the fact that the specimens have been attributed to *Parapapio jonesi* and *P. broomi*. Morphometric analyses indicate a high probability of conspecificity.

Discussion and conclusion

Visual comparison of the virtual rendering of the semicircular canals of Sts 564 and Sts 565 (Figure 1) shows remarkable similarity. In order to assess this similarity quantitatively, dimensions obtained from μXCT scans of these internal anatomical structures, in well-preserved areas of the crania, are particularly valuable.

Unfortunately the edentulous skulls are fragmentary, such that they do not permit detailed analyses of external anatomy of the two specimens. However, morphometric analyses of high-resolution data from μXCT scans of the semicircular canals provide an excellent alternative approach for assessing probabilities of conspecificity. Notably, the delta log se_m value of only 0.03, and the mean log se_m value of -1.73 (less than the mean log se_m of -1.61 and within the lower 95% confidence limit for modern conspecific comparisons), suggest that the holotype specimens of *P. broomi* and *P. jonesi* have a high probability of belonging to the same species. As a hypothesis (H1), we propose that they are conspecific. If correct, the nomen *P. broomi* would have precedence over *P. jonesi*, as the former was described first, by Jones, in 1937. Broom described *P. jonesi* in 1940.

Thackeray and Myer[30] used dental data to question whether specimens attributed to *P. broomi* were those of male individuals, and whether other (generally smaller) specimens attributed to *P. jonesi* were of female individuals. There is no major dietary difference between specimens attributed to either of the taxa, as reflected by stable carbon isotope ratios.[31-33] The isotopic data provide support for the view that a single species is represented by specimens otherwise classified as *P. broomi* or *P. jonesi*. Our morphometric analysis of the type specimens of the two species would seem to confirm this possibility, with the small cranium (Sts 565) possibly being that of a female individual, and the larger specimen (Sts 564) representing a conspecific male specimen of *P. broomi*.

When Trevor Jones first accompanied Robert Broom to Sterkfontein about 80 years ago, Broom picked up the relatively small baboon cranium now catalogued as Sts 565. Almost immediately (after making a cursory examination of the specimen, still encased in breccia), he said something along the following lines: 'Well Jones, thank you for describing a fossil after me. I will return the compliment, and I will name this new baboon after you' (personal communication, Jones to Thackeray, circa 1994). No detailed analyses of the two crania (Sts 564 and Sts 565) had been undertaken at that time. This anecdote reflects the arbitrary manner in which Broom sometimes created new species in the palaeontological record.

It would appear that Broom was being subjective when assessing two specimens of *Parapapio* (Sts 564 and Sts 565) as different species of slightly different size. We have used data from μXCT scans and virtual reconstructions of the semicircular canals of two *Parapapio* crania to test whether they are different at a species level. We conclude that there is a high probability that they are conspecific, based on both log se_m and delta log se_m values. We reiterate the suggestion that the larger of the two (Sts 564) specimens may possibly represent a male individual[30], as the holotype of *P. broomi.* Sts 565 could be referred to the same species, potentially that of a female individual. Here we express these concepts in terms of three hypotheses (H1–H3):

H1: Sts 564 and Sts 565 are conspecific, representing *P. broomi*.

H2: Sts 564 is a male specimen of *P. broomi*.

H3: Sts 565 is a female specimen of *P. broomi*.

The results of our preliminary study of two type specimens, supporting H1, are consistent with the view by Monson et al.[25] indicating that the taxonomic designations of Parapapio and other Plio-Pleistocene Cercopithecidae from South Africa may be 'confounded'. Further analyses, including additional specimens attributed to Parapapio (supplementing our study of Sts 564 and Sts 565, and including specimens attributed to Parapapio cf. jonesi from Ethiopia[34]) are required to address hypotheses of the kind considered in this study.

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