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Morphoarchitectural variation in South African fossil cercopithecoid endocasts

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ABSTRACT

Despite the abundance of well-preserved crania and natural endocasts in the South African Plio-Pleistocene cercopithecoid record, which provide direct information relevant to the evolution of their endocranial characteristics, few studies have attempted to characterize patterns of external brain morphology in this highly successful primate Superfamily. The availability of non-destructive penetrating radiation imaging systems, together with recently developed computer-based analytical tools, allow for high resolution virtual imaging and modeling of the endocranial casts and thus disclose new perspectives in comparative paleoneurology. Here, we use X-ray microtomographic-based 3D virtual imaging and quantitative analyses to investigate the endocranial organization of 14 cercopithecoid specimens from the South African sites of Makapansgat, Sterkfontein, Swartkrans, and Taung. We present the first detailed comparative description of the external neuroanatomies that characterize these Plio-Pleistocene primates. Along with reconstruction of endocranial volumes, we combine a semi-automatic technique for extracting the neocortical sulcal pattern together with a landmark-free surface deformation method to investigate topographic differences in morphostructural organization. Besides providing and comparing for the first time endocranial volume estimates of extinct Plio-Pleistocene South African cercopithecoid taxa, we report additional information regarding the variation in the sulcal pattern of *Theropithecus oswaldi* subspecies, and notably of the central sulcus, and the neuroanatomical condition of the colobine taxon *Cercopithecoides williamsi*, suggested to be similar for some aspects to the papionin pattern, and discuss potential phylogenetic and taxonomic implications. Further research in virtual paleoneurology, applied to specimens from a wider geographic area, is needed to clarify the polarity, intensity, and timing of cortical surface evolution in cercopithecoid lineages.

1. Introduction

Recent research employing three dimensional (3D) imaging techniques has provided important insights into the brain organization of early cercopithecoids and hence Old World monkeys as a

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whole (Gonzales et al., 2015). However, relatively little is known about patterns of cercopithecoid brain evolution more generally, despite the extensive Plio-Pleistocene fossil record. The handful of previous studies has focused mainly on one genus, *Theropithecus* (Falk, 1981; Elton et al., 2001), or estimating endocranial volume (ECV; e.g., Martin, 1993), although more recent work has highlighted the potential utility of examining the internal morphostructure of Plio-Pleistocene cercopithecoids (Beaudet, 2015; Beaudet et al., 2015, 2016). In part, the lack of attention has been because of a paucity of natural endocasts plus methodological limitations in studying cranial material, notwithstanding its abundance. Fortunately, recent advances in the use of high-resolution 3D imaging and computer-assisted analytical approaches have provided the means with which to examine, in much more detail, cranial material from the extensive Old World monkey fossil record and hence fill important gaps in our knowledge of cercopithecoid brain evolution.

The Plio-Pleistocene cercopithecoid record of South Africa samples at least seven cercopithecoid genera and up to 12 species, with fossil material including several complete skulls and/or nearly intact natural endocasts (Freedman, 1957; Szalay and Delson, 1979; Delson, 1984, 1988; Jablonski, 2002; Gilbert, 2007, 2013; McKee et al., 2011). Three *Parapapio* species are currently recognized in South Africa (*Parapapio broomi*, *Parapapio jonesi*, and *Parapapio whitei*) plus the "*Parapapio*" morph identified at Taung and originally attributed to *Parapapio antiquus* (Freedman, 1957; Szalay and Delson, 1979), along with three extinct variants of *Papio*: *Papio angusticeps, Papio izodi*, and *Papio robinsoni* (Freedman, 1957; Delson, 1984; McKee, 1993; McKee and Keyser, 1994). All the *Parapapio* taxa (including some material attributed to *Pp. antiquus*) plus *P. izodi* contain specimens for which endocranial morphology can be assessed. *Theropithecus oswaldi* is also found in South Africa, divided into three chronosubspecies (from oldest to youngest): *Theropithecus oswaldi darti*, *Theropithecus oswaldi oswaldi*, and *Theropithecus oswaldi leakeyi* (Leakey, 1993; Frost and Delson, 2002; Frost, 2007). Although Plio-Pleistocene *Theropithecus* brain evolution has been the subject of previous work (Falk, 1981; Elton et al., 2001), sampling the *T. o. darti* material from Makapansgat is particularly relevant as it was not included in Falk's seminal 1981 study of sulcal patterning and its implications for function and evolutionary history. Aspects of endocranial form can also be studied in *T. o. oswaldi* from Swartkrans, but unfortunately not in two further large-bodied papionin taxa, *Dinopithecus ingens* and *Gorgopithecus major*, as they are represented mainly by fragmentary remains (Freedman, 1957; Delson, 1984; Jablonski, 2002; Jablonski and Frost, 2010). The same is true for specimens from Kromdraai, Makapansgat, and Swartkrans that have been assigned to *Cercocebus* sp. (Eisenhart, 1974; Delson, 1984, 1988). However, it is possible to examine *Cercopithecoides williamsi*, one of two extinct colobine species (the other being *Cercopithecoides haasgati*) recognized in the South African Plio-Pleistocene (Delson, 1984, 1988; Jablonski, 2002; McKee et al., 2011), which provides insight into the colobine as well as the cercopithecine radiation. The fossil monkeys from South Africa are therefore an appropriate and suitably diverse group on which new methodological advances can be applied to increase our knowledge of cercopithecoid brain evolution.

Knowledge of primate brain evolution is based both on comparative information from living species whose brains and behavior can be directly investigated (Armstrong and Falk, 1982) and the interpretation of paleoneurological evidence. To date, much of that paleoneurological evidence has come from the study of endocasts. Fossil endocasts consist of replicas of the internal table of the bony braincase and provide the only direct evidence of brain evolution. When the neurocranium is filled with sediment during fossilization, morphological information about the external brain surface may be preserved as a natural endocast, as illustrated in the South African primate fossil record (Brain, 1981; Holloway et al., 2004). Endocasts constitute a proxy for investigating and quantifying variations in brain size, global brain shape, and neocortical surface morphology, including imprints of cerebral convolutions (i.e., gyri and sulci; Holloway, 1978; Holloway et al., 2004; Falk, 2014; Neubauer, 2014). Given the intimate relationships and patterns of co-variation between brain growth and development and its neurocranial bony container, endocasts are suitable proxies when assessing original brain size and morphological details. Recent comparisons between endocranial organization in the brain and endocranial virtual replicas of primate individuals support the close correspondence between endocranial impressions and cerebral sulci and gyri (e.g., Kobayashi et al., 2014).

Following pioneering research in defining the several levels of evidence that can be collected from endocasts, including gross brain size, delineation of cerebral areas, and major sulcal and gyral identifications (Holloway, 1978), availability of non-destructive penetrating radiation imaging systems, together with recently developed computer-based analytical tools, have allowed for high resolution virtual imaging and modeling of endocranial casts, thus disclosing new perspectives in comparative paleoneurology (Zollikofer et al., 1998; Zollikofer, 2002; Gunz et al., 2009; Weber and Bookstein, 2011). Digital data make the quantitative analysis of overall endocranial shape possible, notably through geometric morphometric methods (Bruner et al., 2003, 2009, 2010; Bruner, 2004; Neubauer et al., 2009, 2010; Gunz, 2015) and registration of surfaces from the correspondence of anatomical landmarks (Specht et al., 2007). However, the use of a traditional methodological toolkit based on landmarks, semilandmarks, and curves, even if efficient in compartmentalizing the endocranial cavity, captures little information about the brain itself and its subdivisions. One potential compromise thus proposed in this study is to combine a detailed analysis of sulcal pattern via automatic detection of the neocortical surface together with the characterization of overall endocranial shape via deformation based-models (Durrleman et al., 2012a, b; Dumoncel et al., 2014; Beaudet, 2015). We also aim to show that the different types of evidence available from endocasts and described by Holloway (1978) can be accessed and assessed reliably for South African fossil cercopithecoid endocrania by means of advanced methods of high-resolution 3D imaging and computer-assisted analytical approaches.

In this paper, along with furthering the development of methods for visualizing and quantifying sulcal pattern and endocranial shape, we report new estimates of ECV (a reliable estimate of actual brain size; Isler et al., 2008) for eight South African cercopithecoid taxa. We also consider the implications of our data on endocranial morphology for improving knowledge of the South African cercopithecoid fossil record, including the taxonomy and evolutionary history of Plio-Pleistocene monkeys, that may be derived from study of sulcal patterns and global shape. We are particularly interested in examining two main issues: (1) variation in sulcal pattern in *Theropithecus*, and (2) the endocranial morphology of *C. williamsi*. Falk (1981) noted distinct features in the sulci of *T. o. oswaldi*, specifically a 'hook-like' configuration of the central sulcus, which was not evident in *Theropithecus gelada*, and by extending the sample to South African fossils, we explore variation and divergence in the *Theropithecus* lineage further, which in turn gives clues to the evolutionary history of that highly successful and widespread Plio-Pleistocene radiation. Other work on sulcal patterning (Connolly, 1950; Radinsky, 1974; Falk, 1978) has also highlighted taxon-based gross sulcal patterning, for example discriminating between colobines and cercopithecines. Further examination of possible cercopithecine/colobine distinctions is