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Upper third molar internal structural organization and semicircular canal morphology in Plio-Pleistocene South African cercopithecoids

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ABSTRACT

Despite the abundance of cercopithecoids in the fossil record, especially in South Africa, and the recent development of morphometric approaches, uncertainties regarding the taxonomic identification of isolated cranio-dental specimens remain. Because cercopithecoids, nearly always found in stratigraphic association with hominin remains in Plio-Pleistocene deposits, are considered as sensitive ecological and chronological biomarkers, a significant effort should be made to clarify their palaeobiodiversity by assessing additional reliable morphological diagnostic criteria. Here we test the relevance of both molar crown internal structure and bony labyrinth morphology for discrimination of fossil cercopithecoid species. We use microtomographic-based 3D virtual imaging and quantitative analyses to investigate tooth endostructural organization and inner ear shape in 29 craniodental specimens from the South African sites of Kromdraai, Makapansgat, Sterkfontein and Swartkrans and provide the first detailed description of the internal structural condition characterizing this Plio-Pleistocene primate assemblage. Our preliminary results show that enamel-dentine junction morphology could be informative for discriminating highly autapomorphic taxa such as *Theropithecus*, while semicircular canal shape is tentatively proposed as an efficient criterion for diagnosing *Dinopithecus ingens*. Further research in virtual paleoprimatology may contribute to the identification of unassigned isolated fossil remains and shed new light on the internal craniodental morphology of extinct primate taxa.

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1. Introduction

Old World monkeys are abundant in the Plio-Pleistocene African fossil record and are one of the best documented primate radiations (Szalay and Delson, 1979; Jablonski, 2002; Jablonski and Frost, 2010). Indeed, probably due to their adaptability, relatively fast life histories and generalized morphology, the phyletic and ecological diversification of the group significantly increased through the Plio-Pleistocene in Africa, and cercopithecoids became dominant primates during this period in Africa (Jablonski and Frost, 2010; Fleagle, 2013). More specifically, the South African karstic cave sites have yielded valuable assemblages of fossil cercopithecoids, documenting potentially seven genera and up to 12 species

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(Freedman, 1957; Szalay and Delson, 1979; Delson, 1984, 1988; Jablonski, 2002; Gilbert, 2007a, 2013; McKee et al., 2011).

Because of their co-occurrence with hominins in paleontological deposits, cercopithecoids provide valuable contextual information regarding hominin paleoecology and biostratigraphic dating, as well as data for the reconstruction of pan-African dispersal patterns and palaeoenvironments (Delson, 1984, 1988; Strait and Wood, 1999; Elton, 2001; Gilbert, 2008; Bettridge and Dunbar, 2012). Also, in the absence of great apes in the Plio-Pleistocene fossil record, cercopithecoids represent the closest relatives to hominins, and they were consequently proposed as a “control-group” for the understanding of evolutionary trends and adaptations of the earliest hominins (Jolly, 1970, 2001; Elton et al., 2001; Elton, 2006). However, the use of cercopithecoids as biomarkers relies on the ability of current diagnostic criteria to taxonomically assign fossil remains and evaluate palaeobiodiversity and relative abundance.

The external craniodental morphology of extinct cercopithecoids has been widely described since the earliest discoveries in South Africa and subsequently used to define fossil cercopithecoid alpha taxonomy (e.g., Freedman, 1957; Maier, 1970; Eisenhart, 1974; Szalay and Delson, 1979; Jablonski, 2002). The most recent reviews of the material available and descriptions of new discoveries and additional specimens have used ‘traditional’ external morphological features and both clarified and expanded the currently accepted taxonomic pattern (e.g., Gilbert, 2013; Gilbert et al., 2015). However, despite the potential value of endostructural information in taxonomic studies, the internal morpho-structural condition of extinct cercopithecoid taxa is reported in only a few studies (e.g., Beaudet, 2015; Beaudet et al., 2015, 2016). If these structures prove to behave as efficient supplementary diagnostic features, their study will offer the opportunity to propose discriminators useful for the identification of isolated and fragmentary craniodental remains, which are abundant in the South African fossil record (see Brain, 1981).

1.1. *Brief review of extinct South African Plio-Pleistocene cercopithecoid taxa*

We follow previous published reviews of South African papionin taxa (e.g., Freedman, 1957; Szalay and Delson, 1979; Jablonski, 2002; Gilbert, 2013) recognizing four species of *Parapapio*, three species of *Papio*, one species of *Dinopithecus*, one species of *Gorgopithecus*, three subspecies of *Theropithecus oswaldi* and one species of *Cercopithecoides*. We confine our review to the taxa included and discussed in our sample.

Parapapio is currently represented in South Africa by three species (*Parapapio jonesi*, *Parapapio broomi*, and *Parapapio whitei*) initially distinguished on the basis of molar size, *Pp. whitei* having the largest and *Pp. jonesi* the smallest teeth (Broom, 1940). Morphologically, *Parapapio* differs from *Papio* by a straight profile of the muzzle dorsum rather than the steep anteorbital drop typically found in the latter (Freedman, 1957; Eisenhart, 1974). In contrast, its teeth are considered morphologically indistinguishable from those of the genus *Papio* (Freedman, 1957) or even from those of other species of Papionini (Heaton, 2006). Also, *Pp. jonesi* displays the least marked development of maxillary ridges and fossae of the *Parapapio* species (Jablonski, 2002; Heaton, 2006). The “*Parapapio*” identified at Taung, originally attributed to *Parapapio antiquus* (Freedman, 1957; Szalay and Delson, 1979), has been recently reassigned to the genus *Procercocebus* based on shared derived features with the *Cercocebus*/*Mandrillus* clade (Gilbert, 2007a, 2013). While some authors, such as Freedman (1957) and Gilbert (2013), followed the same trimodal system as Broom (1940), the validity of the species *Pp. whitei* and *Pp. jonesi* was questioned and Broom's trichotomy challenged by others (Eisenhart, 1974; Thackeray and Myer, 2004; Heaton, 2006; Williams et al., 2007; Fourie et al., 2008).

Three extinct variants of *Papio* have been recognized in South Africa, including *Papio robinsoni*, the largest fossil species in the genus, and the two small-bodied morphs *Papio izodi* and *Papio angusticeps* (Freedman, 1957; Delson, 1984; McKee, 1993; McKee and Keyser, 1994). *Papio robinsoni* is notably characterized by a flat muzzle dorsum and the maxillary ridges raised higher than the nasal bone, whereas *P. angusticeps* has weak maxillary ridges and deep maxillary fossae and teeth shorter and broader than those of *P. robinsoni* (Freedman, 1957). The modern baboon (*Papio hamadryas* sensu lato) was suggested to have emerged from the South African fossil record (Gilbert et al., 2013).

Dinopithecus ingens is a very large and sexually dimorphic fossil baboon species found in the type locality of Schurweberg and at Swartkrans (Delson, 1984; Jablonski, 2002; Jablonski and Frost, 2010). Given numerous craniodental similarities shared with modern baboons, some authors considered *Dinopithecus* to be a subgenus of *Papio* (Freedman, 1957; Szalay and Delson, 1979; Delson and Dean, 1993; Frost, 2001; but see Gilbert, 2013). *Dinopithecus ingens* is distinguished from other papionins by a robust and rugged skull with strong masticatory apparatus, long muzzle and broad interorbital region (Freedman, 1957).

Gorgopithecus major is a large form of baboon characterized by a relatively short, high and narrow muzzle with deep maxillary and mandibular fossae, nearly vertical zygoma and slight sexual dimorphism in the skull (Freedman, 1957; Jablonski and Frost, 2010). This baboon taxon, identified at Kromdraai and Swartkrans (Delson, 1984, 1988), but also in eastern Africa (Gilbert et al., 2016), has been suggested to be phylogenetically related to extant *Lophocebus* (Gilbert, 2013).

The genus *Theropithecus* is distinguished from other papionins especially through its high crowned and columnar-cusped cheek teeth with infoldings of thick enamel and several postcranial features that are related to its terrestrial life (Jolly, 1972; Jablonski, 1993). The species *T. oswaldi* forms a chronolineage 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). *Theropithecus oswaldi darti* is found at Makapansgat, while *T. o. oswaldi* is known at Swartkrans and Sterkfontein (Jablonski, 1993). *Theropithecus oswaldi leakeyi* was identified at Hopefield (Dechow and Singer, 1984) and Bolt's Farm Pit 10 (Gilbert, 2007b).

The extinct colobine species *Cercopithecoides williamsi* is spatially and temporally largely distributed in South African Plio-Pleistocene sites (e.g., Kromdraai, Makapansgat, Sterkfontein, Swartkrans, Taung) (Delson, 1984, 1988; Jablonski, 2002). The cranium displays diagnostic traits such as a rounded calvarium, short and relatively narrow muzzle, and a wide face with large interorbital distance (Freedman, 1957; Jablonski, 2002; key features reviewed in McKee et al. 2011). Teeth are small and exhibit typical colobine features (Szalay and Delson, 1979).

1.2. *Internal craniodental structures as potential diagnostic criteria*

Dental remains are usually the most common material in the primate fossil record (Hartwig, 2002). The identification of isolated teeth or dentognathic fragments is difficult because there are often no distinctive morphological features that can be used to accurately distinguish between closely related taxa. In association with significant improvements in analytical tools, the development of advanced imaging techniques (such as micro-focus X-ray tomography) permits the noninvasive extraction of a wide range of morphostructural information (reviewed in Macchiarelli et al., 2013).

Primate enamel thickness variations were previously suggested to be explained by advantages for resisting fracture and abrasion or for shearing (e.g., Gantt, 1977; Kay, 1981; Dumont, 1995). More

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