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Premolar root and canal variation in South African Plio-Pleistocene specimens attributed to *Australopithecus africanus* and *Paranthropus robustus*

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ABSTRACT

South African hominin fossils attributed to *Australopithecus africanus* derive from the cave sites of Makapansgat, Sterkfontein, and Taung, from deposits dated between about 2 and 3 million years ago (Ma), while *Paranthropus robustus* is known from Drimolen, Kromdraai, and Swartkrans, from deposits dated between about 1 and 2 Ma. Although variation in the premolar root complex has informed taxonomic and phylogenetic hypotheses for these fossil hominin species, traditionally there has been a focus on external root form, number, and position. In this study, we use microtomography to undertake the first comprehensive study of maxillary and mandibular premolar root and canal variation in *Australopithecus africanus* and *Paranthropus robustus* ($n = 166$ teeth) within and between the species. We also test for correlations between premolar size and root morphology as predicted under the 'size/number continuum' (SNC) model, which correlates increasing root number with tooth size. Our results demonstrate previously undocumented variation in these two fossil hominin species and highlight taxonomic differences in the presence and frequency of particular root types, qualitative root traits, and tooth size (measured as cervix cross-sectional area). Patterns of tooth size and canal/root number are broadly consistent with the SNC model, however statistically significant support is limited. The implications for hominin taxonomy in light of the increased variation in root morphology documented in this study are discussed.

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1. Introduction

Premolar tooth root and canal anatomy can vary in structure and size. This variability has been examined in modern humans and non-human hominoids, as well as certain fossil hominins, and has been attributed both functional and systematic significance (Wood, 1981, 1988; Abbott, 1984; Wood et al., 1988; Wood and Engleman, 1988; Tobias, 1995; Brunet et al., 1996; Kupczik et al., 2005; Kupczik and Hublin, 2010; Emonet et al., 2012, 2014; Hamon et al., 2012; Moore et al., 2013, 2015). Nevertheless, limitations in acquiring detailed observations of the roots and canals in situ (Ward et al., 1982; Abbott, 1984; Shields, 2000, 2005) have forced researchers to apply only basic categorizations of morphological variation, thus having an impact on the potential of the premolar root complex for systematic inquiry. Difficulties of imaging the detailed aspects of root structure have also limited our understanding of potential developmental influences on root morphology in modern humans and their fossil relatives.

Examination of the premolar root and/or pulp canals has been accomplished by direct observation (Frisch, 1963; Turner, 1981; Moggi-Cecchi et al., 2010), 2D radiography (Sperber, 1974; Abbott, 1984; Wood et al., 1988; Wood and Engleman, 1988; Shields, 2000, 2005), and 3D computed tomography (Ward et al., 1982; Kupczik et al., 2005; Kupczik and Dean, 2008; Higham et al., 2011; Moore et al., 2013, 2015; Emonet et al., 2014). Compared to the external root(s), the canal system has received less attention either due to experimental design or imaging limitations, but has been examined in extant hominoids (Abbott, 1984; Emonet et al., 2014) and fossil hominins (Kallay, 1963; Sperber, 1974; Abbott, 1984; Wood et al., 1988). More recently, microtomographic

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approaches have identified novel, taxonomically relevant morphotypes in extant ape root/canal morphology and have emphasized the important contribution of the canal(s) for more fine-grained characterization of root morphology (Kupczik and Hublin, 2010; Prado-Simón et al., 2010, 2012; Higham et al., 2011; Moore et al., 2013, 2015). This is particularly relevant as the variable inclusion of both external and internal morphology influences interpretation of taxonomic differences and theorized evolutionary trajectories within clades. For example, studies of premolar root morphology in extant and fossil hominoids have focused on root number or form (Sperber, 1974; Turner, 1981; Tobias, 1995; Emonet and Kullmer, 2011; Emonet et al., 2014), canal number or form (Bermúdez de Castro et al., 1999; Sert and Bayirli, 2004), aspects of the root surface (Turner, 1981; Trope et al., 1986), or a combination thereof (Kallay, 1963; Abbott, 1984; Wood, 1988; Zilberman and Smith, 1992; Higham et al., 2011; Prado-Simón et al., 2012; Moore et al., 2013, 2015). Collectively, these studies highlight the necessity to apply accurate and repeatable scoring criteria of the root system for proper interpretations of variation.

Based on a number of seminal studies (Abbott, 1984; Wood et al., 1988; Wood and Engleman, 1988; Kupczik et al., 2005) and with reference to Miocene fossil apes (see Hartwig, 2002; Emonet, 2009; Emonet et al., 2014), the inferred ‘ancestral’ great ape pattern of the maxillary third (P^3) and fourth (P^4) premolars consists of two buccal and one lingual root, each roughly elliptical in cross-section and containing a single pulp canal. The mandibular third premolar (P_3) bears one mesio-buccal root (elliptical, with a single canal) and one distal root (plate-like, with two canals), and the mandibular fourth premolar (P_4) has one mesial and one distal root (both plate-like, each with two canals). Within the hominin clade, a derived condition of a trend for reduction in root/canal number has been suggested to characterize the genus *Homo* (and the lineage leading to modern humans in particular), while an elaboration (in both form and number) of the mandibular premolar roots has been suggested to be prominent in the genus *Paranthropus* (i.e., ‘molariform’ roots in the robust species of the genus *Australopithecus*, chiefly *Paranthropus boisei*; Abbott, 1984; Wood, 1988; Wood et al., 1988). Moore and colleagues (2013, 2015) analyzed the premolar roots of a large sample of *Hylobates*, *Pan troglodytes*, *Gorilla*, and *Pongo* and demonstrated that while the ancestral pattern is largely retained, each taxon expresses greater variation than previously documented (including unique morphotypes) and there is evidence of both reduction (*Hylobates* and *P. troglodytes*) and elaboration (*Gorilla* and *Pongo*) in root morphology. Re-evaluating the root system of australopiths (see also Abbott, 1984; Wood et al., 1988; Wood and Engleman, 1988), within the context of this newly documented variation in extant apes, is one of the goals of this study.

During root development, morphological variability of the root complex is governed by ontogenetic modification of Hertwig's epithelial root sheath (HERS) and associated inter-radicular process(es) (for review see Butler, 1956; Carlsen, 1967; Kovacs, 1967, 1971; Ten Cate, 1996; Jernvall and Thesleff, 2000; Shields, 2005; Wright, 2007). The sheath begins root formation at the cervical enamel, growing in the direction of and culminating as a primary apical foramen/foramina at the apex of each root body (Kovacs, 1967, 1971; Ten Cate, 1996). Specifically, size of the spherical tooth primordium and cellular activity (i.e., HERS growth and inter-radicular process initiation, level of penetration and unity) interact to regulate root and canal form and number (Jernvall and Thesleff, 2000; Shields, 2005). The resultant co-variation between tooth germ size and root form/number was formulated into a developmental model by Shields (2005) called the root ‘size/number continuum’ (SNC). Based on modern humans, this model predicts that the size of the developing premolar tooth germ (inferred from tooth size) predisposes the number and expression of inter-radicular processes (IRPs) responsible for root form and number (i.e., smaller tooth germs often form fewer roots and larger tooth germs usually form a greater number of roots). However, it has been observed that tooth size alteration does not necessarily correlate with root number variability depending on the ape taxon and premolar position (Abbott, 1984; Shields, 2005; Moore et al., 2015). Therefore, root morphology is postulated to result from complex interactions of genetic, epigenetic, and environmental factors (Kovacs, 1967; Brook and Johns, 1995; Jaenisch and Bird, 2003; Shields, 2005; Brook, 2009; Hamon et al., 2012). The SNC model is testable from the level of the order Primates down to familial twins (Shields, 2005). Recently, Moore and colleagues' (2013, 2015) investigation of the SNC model across extant non-human hominoids (using cross-sectional cervix area as a proxy for tooth size) provided equivocal support for the model, prompting the goal of the present study to investigate its applicability within the hominin clade.

Curiosity about South African australopith premolar root morphology dates back to the mid-20th century, with characterization based mainly from direct examination (e.g., Gregory and Hellman, 1939; Broom and Schepers, 1946; Broom and Robinson, 1952; Robinson, 1956; Sperber, 1974). Previous surveys report differences in root number, form, and orientation distinguishing *Australopithecus africanus* and *Paranthropus robustus* (Robinson, 1956; Sperber, 1974; Abbott, 1984; Wood, 1988; Wood et al., 1988; Wood and Engleman, 1988; Tobias, 1995), as well as evidence for mandibular root ‘molarization’ in cases from Swartkrans and Sterkfontein (Gregory and Hellman, 1939; Broom and Schepers, 1946; Robinson, 1952, 1956; Sperber, 1974; Abbott, 1984; Wood, 1988; Moggi-Cecchi et al., 2006). Comprehensive analyses of the associations of the Sterkfontein Member 4 sample (Moggi-Cecchi et al., 2006), new *P. robustus* material from the site of Drimolen (Keyser, 2000; Moggi-Cecchi et al., 2010), the availability of high-resolution 3D imaging of material from Drimolen, Kromdraai, Makapansgat, Sterkfontein, and Swartkrans, an expanded comparative context of hominoid root morphology (Emonet et al., 2012; Moore et al., 2013, 2015), and new models predicting root variation (Shields, 2005) support a re-examination of root and canal variability in *A. africanus* and *P. robustus*.

The present study uses microtomographic scans of over 95% of the hypodigms of *A. africanus* and *P. robustus* to (1) characterize, quantify, and document variability in premolar root morphology within and between each species, (2) test whether the SNC model adequately explains the observed root variation within each species, and (3) compare our findings with documented variation in extant non-human apes and other Plio-Pleistocene hominins.

2. Materials and methods

The sample of permanent premolars (n = 166; Table 1) is derived from microtomographic scans of crania and mandibles from *A. africanus* (n = 49 individuals) and *P. robustus* (n = 60 individuals). The *A. africanus* specimens originate from Makapansgat and Sterkfontein and the *P. robustus* material originates from Drimolen, Kromdraai, and Swartkrans. All fossil material is curated at

Table 1
Study sample separated by taxon and premolar class.

Taxon	P^3	P^4	P_3	P_4	Total
A. africanus	22	21	16	18	77
P. robustus	22	28	22	17	89
Total	44	49	38	35	166

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