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Abstract: South African hominin fossils attributed to Australopithecus africanus derive from the cave sites of Makapansgat, Sterkfontein and Taung, and from deposits dated between about 2 and 3 million years ago (mya), while Paranthropus robustus is known from Drimolen, Kromdraai and Swartkrans, and from deposits dated between about 1 and 2 million years ago. 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' model (Shields, 2005), which correlates increasing root number with increasing 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, non-metric 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 of increased variation in root morphology documented in this study are discussed.

Dear Dr. Sarah Elton,

Please accept our manuscript entitled *'Premolar root and canal variation in South African Plio-Pleistocene specimens attributed to Australopithecus africanus and Paranthropus robustus'* as a full-length paper for submission to the *Journal of Human Evolution*.

This paper investigates premolar root and canal morphology in an up-to-date sample of *Australopithecus africanus and Paranthropus robustus*. Using microCT we characterize the root complex and also test the existing hypotheses that larger premolars influence root form using measurement at the dental cervix as a proxy for tooth size. That is, larger teeth would likely contain more numbers of roots/canals and possess a larger cervical size when compared to smaller teeth. This study reveals a different pattern of root and canal forms compared to previous reports in the two study taxa and that specific root forms and/or non-metric features occur in each species allowing for distinguishment. Prior research has not had these same results which may be attributed to methodological differences in observation, root form definition and smaller sample size. Within each species, we found general but unanimous evidence that cervical size co-varies with premolar root/canal form. Statistical significance of these variables was only observed in some cases. We conclude that characterizing complex premolar root form is most effectively accomplished through the use of microCT and by 3D observation and that other factors are at play which influence root form. These findings have implications for fossil ape and hominin systematics that are discussed.

Though previous studies have looked at premolar root form in these two fossil taxa, none have done so by 3D methods with a large sample size or examined and categorized both premolar root and canal form/number/configuration with a rigorous definition. The root canals compared to the external appearance of the root, show different and taxonomically important information. We feel this research would be of interest to your readers and we hope that you find it worthy of publication in the *Journal of Human Evolution*.

Thank you for your consideration.

Sincerely,

Collin
N. Collin Moore, MA
Department Human Evolution
Max Planck Institute for Evolutionary Anthropology

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

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Key words: premolar, root, canal, *Australopithecus africanus*, *Paranthropus robustus*, cervical size, dental anatomy, South Africa, Plio-Pleistocene, taxonomy.

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Abstract

South African hominin fossils attributed to *Australopithecus africanus* derive from the cave sites of Makapansgat, Sterkfontein and Taung, and from deposits dated between about 2 and 3 million years ago (mya), while *Paranthropus robustus* is known from Drimolen, Kromdraai and Swartkrans, and from deposits dated between about 1 and 2 million years ago. 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' model (Shields, 2005), which correlates increasing root number with increasing 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, non-metric 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 of increased variation in root morphology documented in this study are discussed.

Maxillary and mandibular premolar tooth roots vary in size and structure, including both root number (and external form) and the number and form of pulp canals within each root. This variability has been examined in modern humans, non-human hominoids, as well as certain fossil hominins, and has been attributed both functional and systematic significance (Wood, 1981; Abbott, 1984; Wood et a., 1988; Wood and Engleman, 1988; Wood, 1988; Tobias, 1995; Brunet et al., 1996; Kupczik et al., 2005; Kupczik and Hublin, 2010; Emonet et al, 2012; Hamon et al., 2012; Moore et al., 2013; Emonet et al., 2014; Moore et al., 2015). Nevertheless, due to limitations in acquiring detailed observations of the roots and canals *in situ* (Abbott, 1984; Shields, 2000, 2005), which has forced researchers to apply only basic categorizations of morphological variation, the potential of the premolar root complex for systematic inquiry in fossil material remains unfulfilled. Difficulties of imaging 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; Higham et al., 2011; Kupczik and Dean, 2008; Moore et al., 2013; Emonet et al., 2014; Moore et al., 2015). 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 approaches have identified novel, taxonomically relevant morphotypes in extant ape root/canal morphology and have highlighted the important contribution of the canal(s) for more fine-grained characterization (Kupczik and Hublin, 2010; Prado-Simón et al., 2010; Higham et al., 2011; Prado-Simón et al., 2012; 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 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, derived conditions 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 *Pan 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; Jernvall and Thesleff, 2000; Shields, 2005; Ten Cate, 2006; 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, 2006). 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 ‘size/number continuum’ (SNC). Based on modern humans, this model predicts that the size of the developing premolar tooth germ directly regulates the number and expression of inter-radicular processes (IRPs) responsible for root form/number (i.e., smaller tooth germs will form fewer roots and larger tooth germs will form a greater number of roots).

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.

Other factors (e.g., epigenetic effects) have also been proposed to influence root number or form, some of which unrelated to size (Kovacs, 1967, 1971; Shields, 2005; Brook, 2009). For example, variables that have been implicated in affecting root morphology include: sexual dimorphism (Schwartz and Dean, 2005; Shields, 2005; Saunders et al., 2007); population variation (Frisch, 1963; Trope et a., 1986; Sert and Bayrili, 2004; Shields, 2005); blood supply and nerve structure (Schwartz and Langdon, 1991; Hildebrand et al., 1995; Moe et al., 2008); cuspal, crown and cervical features or shape (Kovacs, 1971; Wood et al., 1988; White et al., 2000; Haile-Selassie, 2001; Kupczik et al., 2005; Moore et al., 2013); masticatory demands/dietary specialization (Shea, 1983; Spencer, 2003; Kupczik et al., 2005; Taylor, 2006; Kupczik and Dean, 2008; Hamon et al., 2012; Vogel et al., 2014); and canine size and/or jaw size (Wolpoff, 1975; Tobias, 1995; Shields, 2005). Accurately characterizing root variation in the large hypodigms of *Australopithecus africanus* and *Paranthropus robustus* will set the groundwork for assessing the potential influence of some of these factors.

Curiosity in 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 and form between *A. africanus* and *P. robustus* (Robinson, 1956; Sperber, 1974; Abbott, 1984; Wood, 1988; Wood et al., 1988; Wood and Engleman, 1988; Tobias, 1995). For the maxillary premolars, *A. africanus* (Sterkfontein) has a higher frequency of two than three roots (and one case of a single-rooted P^3) compared to *P. robustus* (Swartkrans), which shows the opposite pattern (Robinson, 1956; Tobias, 1995). The *A. africanus* P_3 exhibits only the Tomes' (hereafter referred to as the C-shaped root) form, while *P. robustus* exhibits both the C-shaped and a double rooted form (and one case of three roots) (Robinson, 1956; Sperber, 1974). The C-shaped form for both taxa is described as sometimes having 'partially fused' roots potentially meaning a bifid apex, and both taxa commonly express two rooted P_4s (Robinson, 1956; Sperber, 1974). Inter-specific differences in mandibular root orientation is reported, as well as evidence for root 'molarization' in cases from Swartkrans *and* Sterkfontein (Abbott, 1984; Gregory and Hellman, 1939; Broom and Schepers, 1946; Robinson, 1952, 1956; Sperber, 1974; 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.

Materials and methods

The sample of permanent premolars (n=166) is derived from microtomographic scans of crania and mandibulae 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 (Table 1). All fossil material is curated at either the Ditsong National Museum of Natural History (DNMNH; Pretoria, South Africa; formerly known as the Transvaal Museum), or the Evolutionary Studies Institute, University of the Witwatersrand (Johannesburg, South Africa). Taxonomic attribution of the specimens was acquired from literature sources and museum records. A complete list of the study sample including accession numbers, and taxonomic and premolar class references is listed in Appendix 1.

All specimens were scanned either on a BIR ACTIS 225/300 high-resolution industrial microtomographic system at a spatial resolution of 30–80 μm or a SKYSCAN 1172 desktop microtomographic scanner at a spatial resolution of 30–50 μm. Each tomographic dataset was imported into Avizo (v7.1, www.vsg3d.com) and a threshold-based surface model was created to observe the jaws and dentition of each specimen. In the first instance, left side premolars were selected; if these were missing or damaged to an extent that precluded their analyses, the right side was chosen. On each premolar the sub-cervical region consisting of the radicular dentine and root canal architecture was characterized in 2D from cross-sectional slices oriented perpendicular to the occlusal plane and at various positions along the length of the root body, and/or in 3D from a segmented surface model of the dental tissues (see Moore et al., 2013, 2015). All data collection was performed by NCM.

Root and canal classification

To characterize the form, number and configuration of the root and canal, for each premolar, our methodology followed Moore and colleagues (2013, 2015 developed from methods outlined in Turner, 1981; Abbott, 1984; Chaparro et al., 1999; Vertucci, 2005; Jafarzadeh and Wu, 2007). The terms *root* and *canal* are used in this study to describe an independent element extending from the root trunk and pulp chamber, respectively, and terminating at an apex. When a bi- or trifurcation occurs (i.e., multiple roots/canals), a decision of root or canal number was made by applying the Turner index (1981), which compares the furcation location distance (from inter-radicular summit to root apex) relative to the total root length (from cervix to apex). If this ratio is >25% of the total root length, the root under scrutiny is considered multi-rooted, if <25% it is considered single rooted (possibly with a bifid apex).

Root and canal typology

From the above criteria a classification typology was established combining both the external root surface and canal parameters at each premolar position (following Moore et al., 2013, 2015; and adapted from Abbott, 1984; Brunet et al., 1996; Kupczik et al., 2005; Vertucci, 2005; Jafarzadeh and Wu, 2007; Emonet, 2009; Emonet et al., 2012). Each *root type* consists of a number-letter-number combination. The first number refers to the number of canals, the middle letter indicates canal form/configuration, and the last number provides external root number/form/configuration information that discerns types with the same canal morphology. A formula and description of each root type is listed in Table 2 and this classification is also consistent with variation in premolar root morphology documented in extant hominoids (e.g., Abbott, 1984; Shields, 2000; Kupczik et al., 2005; Moore et al., 2013, 2015).

Tooth size

The size of the tooth cervix is correlated with occlusal crown area (Hillson et al., 2005), root number (Abbot, 1984; Kupczik et al., 2005; Shields, 2005) and canal number (Moore et al., 2013). Therefore, we measured cervical surface area (CSA) as a proxy for tooth size in order to test the predictions of the SNC model (see Moore et al., 2015). CSA was measured on a cross-sectional plane (generated in Avizo) that was positioned initially from points at the buccal and lingual enamel extensions of the cervix. Next, this plane was then adjusted in the mesio-distal aspect until the cervical axis was established perpendicular to the longitudinal axis of the crown and root trunk (cervix to furcation) (following Le Cabec et al., 2012). Finally, this plane was then translated vertically until equidistant between the coronal and apical boundaries of the cervical line (following Olejniczak, 2006). Once the cross-section was properly positioned, the dentine was segmented and the 2D dentine area (mm^2) was calculated in Avizo.

Statistical analyses

A Chi-square test of independence was employed to test for canal/root number and root type differences between the taxa. Nonparametric Mann-Whitney U and/or Kruskal-Wallis one-way analysis of variance tests were used to test for mean CSA differences between the taxa, as well as to test for the relationship between CSA and canal/root number and/or form within each fossil taxon. Statistical analysis was performed using SPSS (v20.0.0, www.SPSS.com) with a significance level of p=0.05.

Results

Root types for each premolar class and taxon

Figures 1–4 illustrate and report counts and percentages of canal and external root form/ number/configuration, as well as a representative cross-sectional image of each root type at each premolar position for *A. africanus* and *P. robustus*. Across the two fossil species, five root types are observed for the maxillary premolars and eight root types for the mandibular premolars. The supplementary material includes a Specimen Image Atlas that illustrates a cross-sectional image of each premolar in the study sample organized by taxon, position and root type. In the following sections and to facilitate clarity of descriptions, root number is described on an ordinal scale (i.e., single, double, triple) and canal number on a numeric scale (i.e., one, two, three, four).

<u>Maxillary premolars</u> The P^3 (Fig. 1) varies in canal number between one (rarely) and more commonly two or three. *A. africanus* exhibits one case (STS 47) of a single elliptical canal and root (1-A-1, 5%) with a slight buccal groove. The frequency of two (2-A) vs. three canals (3-A) is higher in *A. africanus* (45% and 50%, respectively) compared to *P. robustus* (36% and 64%, respectively). Variation in external root number is present in the three canal type in which a small number of specimens (one each in *A. africanus* and *P. robustus*) exhibit a single joined elliptical buccal root with two canals (3-A-1), rather than two independent roots each with one canal (3-A-5). Frequencies of canal/root number and discrete root types did not differ significantly between the taxa (Table 3).

FIGURE 1 HERE

The P^4 (Fig. 2) varies in canal number between two and three. As listed in Table 3, the frequency of two canals (2-A) vs. three canals (3-A) is significantly higher (p=0.001) in *A.*

africanus (62% and 38%, respectively) compared to *P. robustus* (14% and 86%, respectively). Similarly, the frequency of double vs. triple roots differs significantly (*p*=0.001) between the taxa. Both taxa exhibit single cases of the three canal type with joined buccal roots (3-A-1) and *P. robustus* presents one case (SK 28) of joined mesial-buccal/lingual roots (3-A-2).

FIGURE 2 HERE

Mandibular premolars The P_3 canal number varies between one but most commonly two, three and four canals (Fig. 3). There is one *P. robustus* specimen (DNH 58) possessing a single canal/root (1-A-1) with buccal and lingual root grooves and one circular canal that bifurcates periapically (n.b., the root grooves of this specimen are deeply invaginated and differentiate this root form from a typical single rooted premolar in, for example, a modern human). The two canal C-shaped type (2-D-1), with characteristic crescent-shaped mesio-buccal canal and elliptical disto-lingual canal with a bifid apex, is expressed at a similarly moderate frequency for *A. africanus* and *P. robustus* (31% and 33%, respectively). *P. robustus* exhibits other two canal types with one case of a C-shaped type (2-A-3, SKX 311) with circular mesio-buccal and disto-buccal canals and a non-bifid apex, and one case of a two canal, double plate-like root type (2-C-1, TM 1600).

There are key differences in the three canal/double rooted P_3 types between *A. africanus* and *P. robustus* with the former uniquely expressing an elliptical mesio-buccal canal/root (3-A-1, 44%), while only the latter expresses a type with a plate-like mesial canal/root (3-B-1, 47%). In type 3-B-1, the mesial plate-like root relative to the distal plate is narrower lingually, and the buccal edges of both roots are aligned. A three canal type is present in a single *P. robustus* specimen that exhibits triple roots, oriented as two buccal plate-like and one circular lingual root with one canal each (3-C-1, SK 1587a). In this type, the plate-like roots are slightly ‘kidney’ shaped with a groove located on the outward aspect of both the mesial and distal root. The four canal, double plate-like type (4-A-1) is observed only in *A. africanus* at moderate (25%) frequency; the mesial and distal plate-like roots are of similar relative size and appear ‘teardrop’ in shape with the more developed blunt portion extending outward. With regards to taxonomic differences in root type variation for the P_3, there is a significant difference in the frequency distribution of three and four canal premolars ($p<0.001$) due to the unique expression of 3-A-1 (*A. africanus*) and 3-B-1 (*P. robustus*), and lack of the four canal type (4-A-1) in *P. robustus* (Table 3). This difference also drives the significant difference when comparing root type frequency across the whole P_3 sample ($p=0.001$). Ignoring canal number and comparing the frequency of C-shaped roots vs. double roots did not yield significant differences between the taxa ($p=0.508$).

FIGURE 3 HERE

Similar to the P_3, the P_4 (Fig. 4) varies in canal number between one and more commonly two, three and four. One *A. africanus* specimen (STW 87) shows a single canal/root type (1-A-1) that is mesio-distally flattened. The two canal double-plate root type (2-C-1) is expressed in single cases for *A. africanus* and *P. robustus* (each 6%). The two canal C-shaped type (2-D-1) is also expressed in single cases for both taxa. The *A. africanus* C-shaped specimen, STW 212, contains three canals and thus its tentative classification as 2-D-1 emphasizes the external root form rather than canal number. Additionally, *P. robustus* presents a 2-D-1 specimen (SKX 4446) with a root groove that opens on the buccal face (i.e., □-shaped vs. C-shaped). The three canal type (3-B-1) with double plate-like roots is present with moderate frequency in *A. africanus* and *P. robustus* (27% and 23%, respectively), and a single case of a three canal/triple root type (3-C-

1, STS 7) is found only in *A. africanus*. The four canal double plate-like form (4-A-1) is the most prevalent type in both *A. africanus* and *P. robustus* (44% and 59%, respectively). SK 88 is a developing tooth with an incomplete root that was reported as being triple rooted by Sperber (1974). Although not developed enough to be included in this study, we can confirm that it has a separate circular lingual root and a large buccal root whose morphology suggests that it could have ultimately developed into type 3-C-1 (meaning that each taxon would have single examples of this type in the P_4). Inter-specific comparison of all separate root types or between the double root types with three vs. four canals did not differ significantly between the two taxa (Table 3).

FIGURE 4 HERE

Intra-root type variation and additional morphological traits The buccal root of the maxillary premolar type 2-A-2 exhibits two different groove variants when viewed in both cross-section and from a surface model. Among hominoids, Moore and colleagues (2015) outlined four types of groove variants: *type 1*) smooth, circular with no groove; *type 2*) a lingual groove producing a 'C' shaped root; *type 3*) a buccal groove producing a slight '□' shaped root; *type 4*) a compound pattern with grooves on the buccal and lingual (and sometimes mesial and distal) aspects, producing a 'butterfly' or 'X' shape (Figure 5 provides cross-sectional images as examples of types seen in the hominins). The *A. africanus* P^3 exhibits predominately type 2 (7/10, 70%) and a few type 4 (3/10, 30%), while *P. robustus* shows the opposite pattern with only a couple of examples of type 2 (2/8, 25%) and predominantly type 4 (6/8, 75%). The frequency of P^4 groove pattern for *A. africanus* is again predominantly type 2 (12/13, 92%) compared to type 4 (1/13, 8%), but with *P. robustus* at this premolar position being similar in pattern to *A. africanus* with a higher frequency of type 2 (3/4, 75%) than type 4 (1/4, 25%).

FIGURE 5 HERE

Mandibular premolars with bifid apices are common in both taxa for most root types (Table 4). The majority of the P_3 C-shaped (2-D-1) type has a bifid apex for both taxa: *A. africanus* (100%) and *P. robustus* (66%); the single case of type 2-A-3 in *P. robustus* did not have a bifid apex. The P_3 double rooted types express a bifid apex in the distal root in most specimens of *A. africanus* type 3-A-1 (83%) and 4-A-1 (66%), and all of *P. robustus* type 3-B-1 (100%). The *A. africanus* P_4 type 2-C-1 shows no distal bifid apex, whereas the *P. robustus* (100%) specimen does. A distal bifid apex for P_4 type 3-B-1 is uncommon in *A. africanus* (20%) yet typical for *P. robustus* (75%). Similarly, the apices of the P_4 type 4-A-1 were bifid in the majority of *A. africanus* (85% total: 57% distal, 28% both) and *P. robustus* (75% total: 50% distal, 25% both) specimens.

Additionally, in both taxa most double rooted mandibular premolars (type 2-C-1/3-B-1), as well as the P_4 type 4-A-1 with plate-like roots, show an unequal size pattern (see 'moiety relationship', Wood et al., 1988) where the mesial root is often smaller than the distal counterpart (see Fig. 3 and 4). Across the mandibular root types, the plate-like roots are often 'figure-8' or 'kidney' shaped in cross-section (see above) indicating subtle root groove evidence creating the concavity. Finally, the P_3 C-shaped type (2-D-1) is generally distinctive between the taxa and the *A. africanus* version is more consistent in appearance across the sample compared to *P. robustus,* which shows a higher incidence and variable number of grooves on the outer face (see Fig. 6).

FIGURE 6 HERE

Tooth size (CSA) and root type variation within and between taxa

Mean tooth size for each taxon For descriptive statistics of mean tooth size (pooled root types) for each premolar class, see Table 5. Mean tooth size was significantly larger in *P. robustus* compared to the *A. africanus* P^3 (76.20 mm^2 and 63.70 mm^2, respectively; p=0.001) and P^4 (92.50 mm^2 and 72.20 mm^2, respectively; p=0.001). The P_3 in *A. africanus* and *P. robustus* (64.30 mm^2 and 61.60 mm^2, respectively) and the P_4 (74.70 mm^2 and 78.50 mm^2, respectively) did not differ significantly. Tooth size for the P_3 C-shaped type (2-A/2-D) did not differ significantly between the taxa but was slightly larger in *A. africanus* compared to *P. robustus* (63.90 mm^2 and 60.00 mm^2, respectively). For a specimen list separated by each premolar position showing associated root type with tooth size, see Appendix 2 and for summary statistics by tooth see Appendices 3 and 4.

Root morphology and tooth size relationship The variation outlined above allows for the opportunity to test the predictive power of the SNC model within each fossil hominin taxon. Specifically, an increase in cervix size is predicted to be associated with an increase in canal and/or root number. In order to assess canal number, different root types are combined (e.g., double roots with two vs. three vs. four canals). Table 6 presents the results of intra-specific comparisons (e.g., two canals vs. three canals) for each premolar position, indicating whether the difference in tooth size matches the prediction of the SNC model, and whether this trend is statistically significant. Comparisons are limited by sample size and when the sample composition is the same with regards to a comparison of canal or root number, only canal number is reported. Root types of n=1 are reported but excluded from statistical analysis (i.e., only types with $n \geq 2$ are compared).

In the P^3 of *A. africanus* and *P. robustus* there is a non-significant trend for an increase in cervix size between two vs. three canals; however, this trend was more marked in *P. robustus*. In the P^4 of both *A. africanus* and *P. robustus* there is a significant increase in cervical size between two vs. three canals ($p=0.047$ and $p=0.014$, respectively). In the P_3 of *A. africanus* cervical size increases slightly between the C-shaped and double root types, but does not differ significantly; in *P. robustus* these two root types show no size difference. There is also a non-significant trend for a decrease in cervix size in *A. africanus* P_3 double rooted specimens with three vs. four canals. In the P_4, there is a non-significant trend for an increase in cervix size between *P. robustus* specimens with C/□-shaped type vs. those with double roots. In both hominins, P_4 cervical size increases, although non-significantly, between double root types with three vs. four canals.

Comparison with extant non-human hominoids

Inter-specific tooth size, canal number, root type and non-metric trait differences Moore and colleagues (2015) present a detailed overview of premolar root system variability (including both CSA and root type) in living hominoids, and the following section compares these data with the results for *A. africanus* and *P. robustus*. Mean tooth size between the two fossil taxa and extant apes is presented in Table 5. Mean tooth size is significantly different ($p \leq 0.05$) between *A. africanus*/*P. robustus* and each ape genus at most premolar positions (significance was not reached for comparisons of *P. robustus*/*Pongo* P^3, *A. africanus*/*Pongo* P^4 and the P_4 between both fossil taxa and *Pongo*). Figures 7–8 present histograms of canal number and root type frequencies in each taxon separated by premolar position (only types with $n \geq 5\%$ in frequency are listed). The following summarizes the post-hoc pairwise test results between canal number and root type in each of the two hominins compared separately to each extant ape.

For the P^3 (Fig. 7), the hominins differ from the hominoids in exhibiting a greater proportion of specimens with two canals/roots. The most common root type pattern across the sample is type 3-A-5 (triple roots) with type 2-A-2 (double roots) relatively common in the hominins and *Hylobates*. Pairwise tests were significant ($p \leq 0.032$) for all comparisons except between root types in *P. robustus* vs. *Hylobate*s. For the P^4 (Fig. 7), *A. africanus*, *Pan* and *Hylobates* are similar and unique from the other taxa in having a greater proportion of specimens with two canals (2-A), while, *Gorilla* and *Pongo* almost exclusively present three canals (3-A). *P. robustus*, with 14% type 2-A stands intermediate to these groups. This differentiation also holds when comparing root types; although in this case *A. africanus* and *Pan* are differentiated from *Hylobates* in exhibiting type 3-A-1. Pairwise tests were significant ($p \leq 0.040$) in all comparisons except between each hominin vs. *Pan*/*Hylobates*, and *P. robustus* vs. *Pongo*; canal number did not significantly differ between *A. africanus* vs. *Hylobates*.

The P_3 (see Fig. 8) pattern in neither *P. robustus* nor *A. africanus* is matched in any extant taxon in having a larger proportion C-shaped and plate-like double rooted types (i.e., 3-B-1 and 4-A-1, respectively). A variant of the hominin C-shaped form (2-D-1) is observed in *Pan* (2-A-3), but differs morphologically and is less common (see below and Fig. 6). The *A. africanus* four canal form (4-A-1) occurs rarely only in *Pongo*, and the three canal variant in *P. robustus* (3-B-1) is not observed in any extant ape. *A. africanus* and members of Hominidae share the MB + D form, however, canal number frequency is greater compared to *Pan* (two canals, 2-B-1) and lies intermediate to *Pongo*/*Gorilla* (three canals, 3-A-1). Pairwise comparisons were significant ($p \leq 0.001$) for the two fossil taxa except for canal number between both hominins vs. *Pongo*, and *P. robustus* vs. *Gorilla*.

For the P_4 (Fig. 8), all members of Hominidae are dominated by plate-like double rooted types (i.e., 2-C/3-B/4-A). However, *A. africanus* and *P. robustus* are differentiated from the great apes by a much higher relative frequency of four canals (4-A-1) compared to two canals (2-C-1, invariant in *Pan*, common in *Gorilla*/*Pongo*) or three canals (3-B-1, common in *Gorilla*/*Pongo*). The triple rooted (3-C-1) type is rare in both hominins' P_3/P_4 but most common in the *Gorilla* P_3. The single root/canal (1-A-1) type rare in each fossil taxon's P_3/P_4 is most numerous in the *Hylobates* P_4. Pairwise tests were significant ($p \leq 0.006$) for all comparisons.

Across Hominidae, bifid apices in the mandibular premolars of many double rooted types with plate-like roots appears to differ in frequency and sometimes pattern between *A. africanus*, *P. robustus*, *Gorilla* and *Pongo* (see Table 4 and Moore et al., 2015); *Pan* is absent of this feature. In both hominin taxa mandibular type 2-C-1 (i.e., with a single canal per root) does not display a canal isthmus, which is common in the plate-like roots of *Pan*, but absent in other extant hominoids (see Moore et al., 2013, 2015). The C-shaped type (2-A-3) seen in *Pan* displays a rounded, non-bifid apex (note: except one specimen) in contrast to the commonly bifid appearance of this root type equivalent (2-D-1) in the hominin taxa (see previous and Fig. 6).

Discussion

Premolar root and canal variation

The current study documents a greater level of premolar root system variation and a different intra- and inter-specific pattern for *A. africanus* and *P. robustus* than previous investigations (Abbott, 1984; Gregory and Hellman, 1939; Broom and Schepers, 1946; Broom and Robinson, 1952; Robinson, 1956; Sperber, 1974; Wood et al., 1988; Wood and Engleman, 1988; Tobias, 1995). Major trends within and between the two taxa are summarized in Table 7 and specific findings for each are discussed below.

Intra-specific pattern *A. africanus* P^3 root number has been previously reported (Robinson, 1956; Sperber, 1974) as predominantly double (84%) and rarely triple (8%) or single rooted (8%). In contrast, the present P^3 sample exhibits a more similar frequency of double and triple roots (each 45%) and a lower occurrence of single roots (5%). The *A. africanus* P^4 has been reported as exclusively double rooted (Robinson, 1956), however, the present study determined that while double roots are most common (62%), triple roots do occur (33%). Robinson (1956) may have considered the joined three canal type (3-A-1) in the P^3 and P^4 (each 5%) as having double roots (i.e., type 2-A-2). The *A. africanus* P_3 and P_4 are reported as usually expressing the C-shaped form described as having a distinct disto-buccal cleft, as well as cases of double rooted P_4s (Gregory and Hellman, 1939; Robinson, 1952, 1956; Sperber, 1974). The present study confirms this C-shaped form occurs in the P_3 (31%) and P_4 (11%), but also demonstrates the presence of multiple canal, double rooted forms in the P_3 (69%, pooled 3-A-1/4-A-1) and P_4 (77%, pooled 2-C-1/3-B-1/4-A-1) at high frequency, as well as, rare single root/canal (1-A-1), triple canal C-shaped, and triple root (3-C-1) types (each n=1).

The *P. robustus* P^3 and P^4 were reported by Robinson (1956) as predominantly having triple roots (75% and 80%, respectively) and less commonly double roots (25% and 20%, respectively). In contrast to Robinson, our P^3 sample shows a relatively higher frequency of double compared to triple roots (36% and 59%, respectively), while comparatively the P^4 sample is somewhat similar in the ratio of double vs. triple roots (14% and 78%, respectively). Robinson (1956) reports that a few P^3s have 'partially fused' buccal roots, which is consistent with the infrequent (~5%) presence of the 3-A-1 type in the maxillary premolars from our sample.

Robinson (1956:62) also notes the connecting plate of dentine joining the mesio-buccal and lingual roots in SK 28 (3-A-2). The *P. robustus* P_3 has been described as predominantly expressing the C-shaped type with a mesio-lingual cleft (67%) compared to the double root forms (27%, M + D), and rarely (6%) a single root form (Broom and Robinson, 1952; Robinson, 1956; Sperber, 1974). The results of the present study generally agree, but we show a relatively higher frequency of double root types (52%, pooled 2-C-1/3-B-1) that vary in canal number compared to the C-shaped form (38%, pooled 2-A-3/2-D-1). We note the presence of a rare triple root (5%, 3-C-1) type and we concur on the rarity of the single root/canal (5%, 1-A-1) form. The P_4 has been previously reported as typically double rooted (90%, M + D) and rarely (10%) triple rooted (Robinson, 1956; Sperber, 1974). Our results confirm that double root types dominate (88%, pooled 2-C-1/3-B-1/4-A-1); however we report for the first time that these vary in canal number. Furthermore, our analysis identifies previously unreported cases of C/□-shaped (2-D-1) forms (12% total). Recognizing TM 1517 as the *P. robustus* holotype, most other specimens match in terms of root types and tooth size. Additionally, SK 6 originally named *P. crassidens* (Broom, 1949; Broom and Robinson, 1952) is now generally accepted within the *P. robustus* hypodigm (see Wood et al., 1988 and references therein) and does not display unusual premolar root morphology or size compared with other specimens of the taxon.

Inter-specific pattern Our results concur with previous studies (Broom and Schepers, 1946; Broom and Robinson, 1952; Robinson, 1956; Sperber, 1974; Wood et al., 1988; Wood and Engleman, 1988; Tobias, 1995) that maxillary premolar canal/root number tends to be greater in *P. robustus* than *A. africanus*, however, we demonstrate that this is more apparent for the P^4 than P^3. In the mandibular premolars, the P_3 rather than the P_4 is more informative for distinguishing between *A. africanus* and *P. robustus* (see Fig. 3 and Table 7). Similar to prior reports of the P_3

C-shaped form (i.e., 2-A-3/2-D-1), our sample shows a slightly higher frequency in *P. robustus* (38%) than *A. africanus* (31%) and also highlights the distinctive inter-specific morphology in this root type (see Fig. 6 and Table 7). However, we demonstrate that both hominins more commonly exhibit double rooted P_3s, which additionally are taxonomically distinctive (i.e., type 3-A-1/4-A-1 in *A. africanus* vs. type 3-B-1 in *P. robustus*). The distinguishing feature between these root types involves the orientation and form of the mesial root relative to the distal root (3-A-1, MB elliptical + D plate-like vs. 3-B-1/4-A-1, M + D plate-like) or canal number (3-A-1/3-B-1, three canals vs. 4-A-1, four canals). Gregory and Hellman (1939) state that the *Paranthropus (P. robustus*) P_3 appears similar to the *Plesianthropus* (*A. africanus*) P_4 and are likely referring to the plate-like morphology (i.e., P_3 type 4-A-1 and P_4 types 2-C-1/3-B-1/4-A-1). Our study confirms that mandibular root 'molarization' occurs within the Swartkrans and Sterkfontein assemblages (Robinson, 1956; Sperber, 1974; Moggi-Cecchi et al., 2006). Maxillary premolar double root buccal groove patterning (see Results and Fig. 5) is previously unreported and appears to differ (albeit non-significantly) between the two taxa. Future study should examine this phenomenon across primates (see also Moore et al., 2015) to further elucidate taxonomic patterns of this trait.

Based on analyses of craniodental morphology, *A. africanus* and *P. robustus* are often referred to as gracile and robust australopiths, respectively (Wood and Stack, 1980; McCollum, 1999; Wood and Constantino, 2007; Gunz, 2012). In establishing this dichotomy, craniomandibular characters, endocast volume, relative anterior, canine, and post-canine tooth size, relative premolar crown size, enamel thickness, and premolar root number/form (specifically with reference to East African *P. boisei*, discussed below) has led the robust taxa (including *P. aethiopicus*) to be allocated by cladistic analysis to a monophyletic clade within the hominin lineage (Rak, 1983; Chamberlain and Wood, 1987; Grine and Martin, 1988; Wood, 1988; Strait and Grine, 2004; Gunz, 2012). Specifically, premolar root morphology in the robust taxa (i.e. *P. boisei*) is characterized as 'molariform' with the P_3 and P_4 roots appearing plate-like (usually with two canals in each plate) and resembling those of the molars (Abbott, 1984; Wood, 1988; Wood et al., 1988). In our study, some P_3s of both species exhibit a 'molariform' appearance with plate-like forms (i.e., 2-C-1/3-B-1/3-C-1/4-A-1), but to differing degrees. *P. robustus* exhibits a greater frequency of plate-like P_3s compared to *A. africanus* and may be considered more derived. Both taxa also express low numbers of the mandibular premolar triple rooted type (3-C-1, see also *A. bahrelghazali* below). It appears that premolar root 'molarization' does not typify the robust autralpiths (Moore et al., 2015; this study; see also *Gorilla*/*Pongo* above and *A. afarensis* below) and future investigation should determine the extent of this character state within the hominin clade as it has phylogenetic connotations.

Our results are relevant for the debated hypothesis that a larger-toothed *Australopithecus* species (distinct from *A. africanus* and referred to as *A. prometheus*) could be present in Member 4 of Sterkfontein (e.g., Fornai et al., 2010; Clarke, 2013; Grine, 2013; Grine et al., 2013). Specimens from our sample that have been proposed, based on aspects of crown morphology and size, to differ from *A. africanus* include: STS 1, 36, and 71 and STW 183, 252, 384 and 498 (Clarke, 1985, 1989, 1994a, 2008; Fornai et al., 2010). In our analysis STS 1, 36 and 71, and STW 183, 252 and 384 do not display distinctive patterns of root morphology, but are well above the mean CSA for their respective premolar positions, especially the latter two specimens. STW 498 along with 142, 212 and 401 (see also Moggi-Cecchi et al., 2006) express the P_3 double-plate/quad-canal type, which is not observed elsewhere in the sample. However, species of *Pongo* variably express this P_3 root type, a wide range of variation is documented in differing populations among modern humans (Trope et al., 1986; Sert and Bayrili, 2004; Shields, 2005), and a large cervical size range occurs within non-human apes (see Table 5), thus, a conservative interpretation of premolar root variation would suggest that Member 4 individuals belong to a single species (see also Kimbel and White, 1988; Moggi-Cecchi, 2003; Moggi-Cecchi et al., 2006; Grine, 2013; Grine et al., 2013).

Comparison with Plio-Pleistocene hominins

With some obvious taxonomic differences, the root types documented for *A. africanus* and *P. robustus* share many similarities with other Plio-Pleistocene non-*Homo* hominin taxa. Root type frequencies and counts presented below are based from specimen description/counts in published literature (note: due to historical methodological limitations, canal information is rarely available for many hominin taxa) or from specimen images/illustrations.

The P^3 single canal/root type is present in a single *A. africanus* specimen (Robinson, 1956; Tobias, 1995; this study) but is not reported for other non-*Homo* hominins during this time period. A two canal/double rooted P^3 is present in *A. deyiremeda* (BRT-VP-3/1, Haile-Selassie et al., 2015) and *A. sediba* (MH 1/2, Irish et al., 2013). The relative frequency of a two canal/double rooted P^3 is higher in *A. africanus* compared to *A. anamensis* (25% from Coffing et al., 1994; Leakey et al., 1995; Ward et al., 2001, 2013) and *A. afarensis* (17% from Johanson and White, 1979; White, 1977, 1980; Ward et al., 1982), while triple root P^3s are most prevalent in *P. boisei* (90% from Tobias, 1967; Wood, 1991; Alemseged et al., 2002; Domínguez-Rodrigo et al., 2013). Triple rooted P^3s are also reported for all three specimens (KNM-WT 38343A, 38350, 40000) of *K. platyops* (Leakey et al., 2001) and *A. bahrelghazali* (KT 12/H2, Brunet et al., 1996).

The *A. africanus* two canal/double root P^4 is higher in frequency compared to *A. anamensis* (50%) and *A. afarensis* (33%) (White, 1977; Ward et al., 1982; White et al., 2006; Ward et al., 2013), and is present in one *K. platyops* specimen (KNM-WT 38350) that may bifurcate apically (Leakey et al., 2001), and also *A. deyiremeda* (BRT-VP-3/1, Haile-Selassie et al., 2015). *K. platyops* (KNM-WT 40000) also presents the triple root P^4 (Leakey et al., 2001) and this type is ubiquitous in *P. boisei* (100%) and reported as present in *Ar. ramidus* (ARA-VP-1/3000) (Tobias, 1967; Wood, 1991; Alemseged et al., 2002; Suwa et al., 2009; Domínguez-Rodrigo et al., 2013). Compared to other early hominins, type 3-A-1 (with joined buccal roots) is higher in frequency (66%) in *A. afarensis* P^3s (Ward et al., 1982) and potentially present in both *S. tchadensis* maxillary premolars (TM 266-01-060-01); the latter is described as having "three pulp canals and two roots" (Brunet et al., 2002:150).

The P_3 C-shaped type observed with moderate frequency in *A. africanus* and *P. robustus* is also reported for *Ar. ramidus* (ARA-VP-1/3000, White, 2002) and in the P_3/P_4 of *A. deyiremeda* (WYT-VP-2/10, Haile-Selassie et al., 2015). Ward and colleagues (1982) note that 30% of *A. afarensis* P_3s exhibited a single 'dumbbell-shaped' root body with two canals, and it remains to be determined if these specimens would classify under the 2-D-1 type defined in this study. *P. robustus* expresses a single case of the P_4 C-shaped type as does the single P_4 of *Ar. kadabba* (Haile-Selassie et al., 2001). The single case of the *A. africanus* P_4 three canal C-shaped type appears similar to those reported for the Atapuerca-TD6 remains (Bermúdez de Castro et al., 1999). The rare *P. robustus* □-shaped type has not been noted in prior fossil hominin literature. Without considering canal number, the P_3 MB + D type is rare in *A. afarensis* (6%), moderate in *P. boisei* (33%) and *A. africanus* (44%), and highest in *A. anamensis* (67%) (Johanson and White, 1979; Wood et al., 1988; Coffing et al., 1994; this study). Three canals within a MB + D type (3-A-1) is reported for *A. anamensis* (29%, Ward et al., 2001, 2013) and is the only type reported for *S. tchadensis* (Brunet et al., 2005).

Some double rooted P_3 types have been described for *A. afarensis, A. anamensis, A. deyiremeda* and *A. sediba*, which do not seem to correspond with those in *A. africanus* and *P. robustus*. For example, *A. afarensis* shows a high frequency (55%) of a B + L type (Ward et al., 1982) that is also seen in *A. deyiremeda* (BRT-VP-3/14, Haile-Selassie et al., 2015), while *A. anamensis* is described as possessing a B + DL type (n=1) with what appears to be a plate-like mesial root and the distal root has a high bifurcation (KNM-KP 47951, Ward et al., 2013). *A. sediba* is noted as having a double rooted Tomes' variant (MH 1, Irish et al., 2013). The P_3 M + D plate-like, four canal type (4-A-1) present in four *A. africanus* P_3s matches the description for 67% of *P. boisei* specimens (Abbott, 1984:338; Wood et al., 1988). The *P. robustus* P_3 three canal/double plate-like root form (3-B-1) has not been specifically reported in other fossil hominin taxa. Excluding canal information, the P_3 plate-like root types are also observed from published images in a single *A. afarensis* (White et al., 2000) and possibly *Ar. ramidus* specimens (Suwa et al., 2009).

Within the P_4 double plate-like root (M + D) configuration, canal number differs inter-specifically, with the two studied taxa presenting two, three, and most commonly four canals. *A. afarensis* (Ward et al., 1982) and *P. boisei* (Wood et al., 1988) are described as having a high frequency of four canals (84% and 100%, respectively), as does one specimen of *A. deyiremeda* that also appears to have a high distal bifurcation (BRT-VP-3/14, Haile-Selassie et al., 2015). A single *A. anamensis* specimen presents four canals (Ward et al., 2013), while the two *S. tschadensis* specimens exhibit three canals (Brunet et al., 2002, 2005). The mandibular premolar single canal/root type (1-A-1) is observed rarely (n≤2) in *A. africanus*, *A. anamensis* and *A.*

afarensis (Robinson, 1956; White, 1977; Coffing et al., 1994; this study) but is reported for the *Ar. ramidus* P_4 (White et al., 1994). Triple rooted mandibular premolars appear as rare (n=1) in *A. anamensis*, *A. afarensis* and *A. africanus* (White, 1977, 1980; Ward et al., 1982; this study), but is reported for both *A. bahrelghazali* mandibular premolars (Brunet et al., 1996); excluding *A. africanus*, it is unclear if all the latter specimens would be classified as type 3-C-1.

While both *A. africanus* and *P. robustus* show reduced maxillary premolar root/canal number from the inferred ancestral great ape condition (i.e., reduction in number from three to two roots), *A. africanus* exhibits more reduction than *P. robustus*. In contrast, the *A. africanus* mandibular premolars display the highest proportion root types common with extant apes (i.e., P_3 MB + D, P_4 M + D), whereas *P. robustus* shows no evidence of this type in the P_3. Both taxa exhibit similar frequencies of P_3 reduction (i.e., reduction in number from two to one root) in the C-shaped form despite also exhibiting the 'molariform' condition (see above); extant apes do not exhibit this mixture. The double rooted P_4 (M + D) remains largely stable across the study fossil and extant taxa, although the hominins show comparatively greater canal numbers. With some exceptions, the ancestral condition ubiquitous in extant great apes (Abbott, 1984; Moore et al., 2015) contrasts with the relatively higher frequency of the two derived conditions present in each study hominin, indicating that the two lineages broadly differ in developmental processes regulating root morphology (see also Wood, 1988). The increasing availability of microtomography offers a new opportunity to revisit premolar root and canal variation in the hominin clade in order to incorporate the level of detail demonstrated in this study to be wholly taxonomically informative.

The developmental basis of root formation and morphological variation

Aspects of HERS growth and IRP number, orientation, and relative timing of development can be inferred from the study of fully formed roots and canals, and compared between hominin species (Butler, 1956; Carlsen, 1967; Kovacs, 1967, 1971; Turner, 1981; Abbott, 1984; Wood, 1988; Wood et al., 1988; Jernvall and Thesleff, 2000; Shields, 2005; Ten Cate, 2006; Wright, 2007). The greater frequency of maxillary premolar double vs. triple root/canal types in *A. africanus*, as opposed to *P. robustus*, indicates a higher occurrence of buccal IRP suppression responsible for bifurcating the dentine and canal into two roots. More subtle IRP activity is seen in the double root/canal maxillary premolar root groove variants (type 2 and 4), and the bifid apices common in the mandibular premolars. On the buccal root (and sometimes canal) of the maxillary premolar root groove type 2, an IRP induces slight penetration on the lingual aspect, while in type 4, multiple IRPs are present primarily on the buccal and lingual, and sometimes mesial and distal aspects. Mandibular premolar apical bifidity suggests the presence of IRP union occurring only during the last or penetrative phase of root development (post-crown eruption and occlusion) which may spatially accommodate nerves traversing the mandibular body (Pell and Gregory, 1933; Kovacs, 1967, 1971). Many of the plate-like forms with a ‘figure-8’, ’kidney’ or ’teardrop’ appearance is evidence of subtle IRP and root sheath activity that produces such morphology (including the $P^{3/4}$ joined types).

Across the sample, several root types exhibit multiple canals within one root body in both maxillary (3-A-1/3-A-2) and mandibular (2-D/3-A/3-B/4-A) premolars indicating a tendency for IRP suppression on the outer root, but not in expression of individual canals. For example, the C-shaped types (i.e., 2-A/2-D) exhibits partial inhibition of the disto-buccal IRP but not of the lingual IRP given the generally rounded outer face with developmental grooves and characteristic deep inner cleft, respectively (Shields, 2000; Moore et al., 2015; this study);

however, in many cases the IRPs eventually unite periapically resulting in a bifid appearance. This process would be reversed in the □-shaped type and may indicate epigenetic influences of the developing root causing root sheath and IRP pattern inversion (see Shields, 2005; Brook, 2009). Additionally, type 2-D-1 vs. 2-A-3 show canal shape differences that correspond to variation in root sheath growth; in the former root type, partial invagination in the mesio-buccal canal results in the 'crescent' shape not seen in the latter type. The inter-specific difference in the outward appearance of the C-shaped type (2-D-1, see Results and Fig. 6) is indicative of subtle root sheath and IRP differences unique to *A. africanus* and *P. robustus* resulting in multiple root grooves in *P. robustus*, compared to the singular, broad concavity in *A. africanus* (see Fig. 6).

The P_3 double root, multi-canal types 3-A-1, 3-B-1 and 4-A-1 each stem from unique developmental modifications of the mesial root and canal (see also Wood, 1988). The *P. robustus* type 3-B-1 compared to 3-A-1 in *A. africanus* exhibits mesio-distal compression, bucco-lingual expansion and mesial reorientation (i.e., parallel M + D roots instead of oblique MB + D roots) of the mesial root sheath; this results in a 'molariform' appearance of the root and canal, but no invagination leading to an increase in canal number (i.e., as in type 4-A-1) (see also Abbott, 1984; Wood et al., 1988). Conversely, the plate-like types with one vs. two mesial canals in *P. robustus* compared to *A. africanus* (3-B-1 and 4-A-1, respectively) indicates generally similar outer root sheath regulation (i.e., shared plate-like mesial root); however, type 4-A-1 differs through additional mesial canal partitioning (i.e., dentine deposition) resulting in two circular canals instead of one flattened canal as in 3-B-1. Within *A. africanus*, type 4-A-1 vs. 3-A-1 indicates mesial root sheath and canal number modification of the double rooted types not observed in *P. robustus*. These differences in root configuration and canal number may be reflections of intra- and inter-specific variability in crown, cuspal, cervical and/or EDJ morphology influencing HERS (Wood et al., 1988; White et al., 2000; Haile-Selassie, 2001; Kupczik et al., 2005; Skinner et al., 2008; Moore et al., 2013). Future research should more thoroughly investigate the developmental relationship between crown and root morphology.

The rare single root/canal type (1-A-1) indicates inhibition of invagination on the canal portion, but limited IRP activity on the outer root surface as some developmental grooves are observable on specimens of *A. africanus* and *P. robustus* (see Figs. 1, 3 and 4, and supplementary material). It is unclear whether minor invaginations represent poorly formed IRPs or reduced cell division in the root sheath. The rare triple root/canal type (3-C-1) uniquely shows three IRPs corresponding to the number of features forming two plate-like and one circular root. Across the sample, in mandibular premolar double rooted types, the number of canals equaling the number of roots is rare (n.b., 2-C-1); this indicates that in both fossil taxa, HERS activity creating multiple canals (particularly in the distal root) is common. Future study should focus on the incongruence of canal and root morphology and what role nerve and blood supply have on the developing root system and resulting morphology (see Moe et al., 2008).

Developmental implications of the SNC in A. africanus and P. robustus with comparison to extant hominoids

Our results for *P. robustus'* larger maxillary premolar mean tooth size (i.e., cervical surface area) compared to *A. africanus* concur with previous assessments using maximum crown area (calculated from MD/BL linear measurements from Robinson, 1956; Sperber, 1974; Moggi-Cecchi et al., 2006) or crown base area (Wood and Engleman, 1988). Tooth size variation (CV, see Table 5) in the *A. africanus* P^3 and P^4 is larger than *P. robustus* and may be attributed to the more variable root/canal numbers in the expanded sample. Based on maximum crown diameter, prior studies (Robinson, 1956; Sperber, 1974; Moggi-Cecchi, 2006) report that *P. robustus* exceeds *A. africanus* at every premolar position. The current study (using cervical surface area) is in agreement, with the exception that the P_3 is slightly larger (4.38%) in *A. africanus* vs. *P. robustus*. The *P. robustus* P_4, however, is larger than *A. africanus*, which concurs with prior investigation (Robinson, 1956; Sperber, 1974; Moggi-Cecchi, 2006). P_3 tooth size variation (CV) is larger in *P. robustus* compared to *A. africanus*, while the opposite is seen in the P_4; like the maxillary premolar CV pattern (*A. africanus* > *P. robustus*), this result may stem from the comparatively greater canal number variability in the *A. africanus* P_4 vs. the *P. robustus* P_3.

The SNC model has been applied to non-human apes (Moore et al., 2013, 2015) with mixed intra-specific results. Intra-specific analysis for both *A. africanus* and *P. robustus* provide several instances supporting the SNC model (Table 6). For both taxa, P^4s with double roots are significantly smaller than those with triple roots, and the P^3 exhibits a similar, but non-significant size trend. The mandibular premolar intra-specific relationship is less clear. In several instances, these results yield a positive size trend in canal/root number (i.e., the P_4) but this size difference can be negligible or nonexistent as between the P_3 C-shaped vs. double root types. *A. africanus'* P_3 double root types with three vs. four canals had a negative size trend that contradicts Shields' model (2005). It should be noted that these findings may be due to small sample sizes for some root types. These results (along with those for extant apes) suggest that intra-specifically, tooth germ size variation can predict root/canal number or form but that in a number of cases germ size/cell number and IRP number (i.e., union producing two separate roots) can be decoupled.

Finally, it has been inferred that dietary strategies (i.e., omnivory) and food processing (e.g., stone tool use) differ between extant apes and early hominins as a group (Robinson, 1972; Fleagle, 1998; McHenry and Coffing, 2000; Skinner et al., 2015). The premolar pattern observed in the study hominins vs. extant apes may be indicative of a high proportion of hard/brittle/abrasive foods (i.e., hard fruits, seeds, USOs, grasses, sedges), animal protein, fall-back foods and a seasonally changing diet (Unger and Grine, 1991; Sponheimer and Lee-Thorp, 1999; Sponheimer et al., 2006; Henry et al., 2012, Sponheimer, 2013). The wider dietary niche of the fossil taxa may explain the suite of conditions (and convergence in morphologies, see above) despite their cervical size closeness with *Pongo*. Future research should attempt to link premolar root morphology with the material properties of food and determine what adaptive significance this confers (i.e., finite element modeling, see Benazzi et al., 2011).

Conclusions

Our analysis of premolar root and canal form/number/configuration in *A. africanus* and *P. robustus* reveals increased levels of variation but also taxonomically distinctive morphology at particular premolar positions. Canal morphology, examined using microtomography, is an important trait and augments the inter-specific differences based on external root appearance alone. At some premolar positions our results support the ‘size/number continuum’ model within species, particularly in the maxillary premolars. *A. africanus* and *P. robustus* differ in their patterns of reduction/elaboration from the inferred ancestral ape condition at particular premolar positions. Future studies should synthesize the relationship between the root system and dental tissue proportions, crown and EDJ morphology, jaw architecture and dietary complexity across Plio-Pleistocene hominins. These findings provide a framework for the evaluation of root and canal morphology in fossil hominins and characters incorporated into cladistic analysis.

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Figure 1: Canal and root variation frequency (in percent) in the upper third premolar (raw counts are in brackets). Examples of each root type in cross-section are illustrated at bottom. Cross-sectional images of specimens arranged to reflect anatomical orientation legend (in upper left corner).

Figure 2: Canal and root variation frequency (in percent) in the upper fourth premolar (raw counts are in brackets). Examples of each root type in cross-section are illustrated at bottom. Cross-sectional example images arranged to reflect anatomical orientation legend (in upper left corner).

Figure 3: Canal and root variation frequency (in percent) in the lower third premolar (raw counts are in brackets). Examples of each root type in cross-section are illustrated at bottom. Cross-sectional example images arranged to reflect anatomical orientation legend (in upper left corner). *canals arranged mesio-buccal and disto-lingual.

Figure 4: Canal and root variation frequency (in percent) in the lower fourth premolar (raw counts are in brackets). Examples of each root type in cross-section are illustrated at bottom.*contains three canals (STW 212 (243)) included; **SKX 4446 is □-shaped. Cross-sectional example images arranged to reflect anatomical orientation legend (in upper left corner).

Figure 5: Variation in maxillary premolar buccal root groove morphology (type 2-A-2): type 2 (A) and type 4 (D); less developed example on left and well developed example on right.

Figure 6: Variation in the C-shaped root type in *Pan* (top), *A. africanus* (middle) and *P. robustus* (bottom); all specimens are the P_3 unless indicated. Cross-sectional example images arranged to reflect anatomical orientation legend (in upper left corner).

Figure 7: Upper third and fourth premolar canal number and root type distribution across *A. africanus*, *P. robustus* and non-human extant hominoids.

Figure 8: Lower third and fourth premolar canal number and root type distribution across *A. africanus*, *P. robustus* and non-human extant hominoids.

Supplementary Material - Specimen Image Atlas: Presents a mid-root cross-sectional image of each fossil specimen divided by taxon, premolar position and root type. Specimen orientation observed from the occlusal aspect. Dashed lines emphasize morphology due to poor contrast and/or indicate that root presence was inferred by existing morphology. 1–indicates three canal type 2-D-1; 2–indicates rotated root entities; 3–indicates roots partially appressed, but not joined; 4–indicates □-shaped type 2-D-1.

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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

TABLE 2. Classification scheme for premolar canal and root types

Root Type	Canal Number	Root Number	Formula	Description
				P^3/P^4
1-A-1	1	1	1_1	1 elliptical root / 1 elliptical canal
2-A-1	2	1	$1_{2\ (1B+1L)}$	1 elliptical root (joined 1B + 1L roots) / 2 circular canals (1B + 1L)
2-A-2	2	2	$1_1B + 1_1L$	2 roots (1B elliptical + 1L circular) / 2 circular canals (1B + 1L)*
3-A-1	3	2	$1_2B + 1_1L$	2 roots (1B elliptical + 1L circular) [joined 2B roots] / 3 circular canals (2B + 1L)
3-A-2	3	2	$1_2ML + 1_1BD$	2 roots (1ML plate-like + 1BD circular) [joined 1MB +1L roots] / 3 circular canals (2ML + 1BD)
3-A-3	3	2	$1_1MB + 1_2DL$	2 roots (1MB circular + 1DL plate-like) [joined 1DB +1L roots] / 3 circular canals (1MB + 2DL)
3-A-4	3	1	$1_{3\ (2B+1L)}$	1 root (joined 2B + 1L roots, tripartite cross-section) / 3 circular canals (2B + 1L)
3-A-5	3	3	$2_2B + 1_1L$	3 roots (2B elliptical + 1L circular) / 3 circular canals (2B + 1L)
4-A-1	4	3	$2_2B + 1_2L$	3 roots (2B circular + 1L plate-like) / 4 circular canals (2B + 2L)
				P_3/P_4
1-A-1	1	1	1_1	1 elliptical root / 1 elliptical canal
1-B-1	1	1	$1C_1$	Tomes' root; 1 C-shaped root body (deep ML groove, round DB face) / 1 C-shaped canal
2-A-1	2	1	$1_{2\ (1M+1D)}$	1 elliptical root (slight B + L grooves) [joined 1M + 1D roots] / 2 circular canals (1M + 1D)
2-A-2	2	2	$1_1M + 1_1D$	2 circular roots (1M + 1D) / 2 circular canals (1M + 1D)
2-A-3	2	1	$1C_{2\ (1MB+1DL)}$	Tomes' root; 1 C-shaped root body (deep ML groove, round DL face) / 2 circular canals (1MB + 1DL)
2-A-4	2	1	$1\text{Ɔ}_{2\ (1MB+1DL)}$	Reverse Tomes' root; 1 Ɔ-shaped root body (deep MB groove, round DL face) / 2 elliptical canals (1MB + 1DL)
2-B-1	2	2	$1_1MB + 1_1D$	2 roots (1MB elliptical + 1D plate-like) / 2 canals (1MB elliptical + 1D plate-like)
2-C-1	2	2	$1_1M + 1_1D$	2 plate-like roots (1M + 1D) / 2 plate-like canals (1M + 1D)
2-D-1	2	1	$1C_{2\ (1MB+1DL)}$	Tomes' root, usually bifid apex; 1 C-shaped root body (deep L groove, slight groove(s) on M, B or D aspects of round outer face) / 2 canals (1MB crescent + 1DL elliptical)**,***
3-A-1	3	2	$1_1MB + 1_2D$	2 roots (1MB elliptical + 1D plate-like) / 3 canals (1MB elliptical + 2D circular)
3-B-1	3	2	$1_1M + 1_2D$	2 plate-like roots (1M + 1D) / 3 canals (1M plate-like + 2D circular)
3-C-1	3	3	$2_2B + 1_1L$	3 roots (2B plate-like + 1L circular) / 3 canals (2B elliptical + 1L circular)
4-A-1	4	2	$1_2M + 1_2D$	2 plate-like roots (1M + 1D) / 4 circular canals (2M + 2D)

Note: Formula column standard numbers denote root number and subscript numbers denote canal number.

*variable B root groove morphology.

**STW 212 (STW 243) specimen exhibits an additional canal (3 canals) and trifid apex.

***SKX 4446 specimen exhibits a Ɔ-shaped configuration.

TABLE 3. Variation in canal/root number and selected root types between taxa for each premolar class

Comparison	*A. africanus*	*P. robustus*	Chi-square	*p*-value
P^3				
2 vs. 3 canals (2-A vs. 3-A)	10/11	8/14	0.559	0.455
2 vs. 3 roots (2-A/3-A-1 vs. 3-A-5)	11/10	9/13	0.568	0.451
Discrete types (1-A-1 vs. 2-A-1 vs. 3-A-1 vs. 3-A-5)	1/10/1/10	0/8/1/13	1.614	0.656
P^4				
2 vs. 3 canals (2-A vs. 3-A)	13/8	4/24	12.010	0.001
2 vs. 3 roots (2-A/3-A-1/3-A-2 vs. 3-A-5)	14/7	6/22	10.166	0.001
Discrete types (2-A-2 vs. 3-A-1 vs. 3-A-2 vs. 3-A-5)	13/1/0/7	4/1/1/22	12.784	0.005
P_3				
1 vs. 2 roots (2-A/2-D vs. 2-C/3-A/3-B/4-A)	5/11	8/11	0.438	0.508
3 (MB + D) vs. 3 (M + D) vs. 4 canals (M + D) [3-A vs. 3-B vs. 4-A]	7/0/4	0/10/0	23.521	<0.001
Discrete types (1-A-1 vs. 2-A-3 vs. 2-C-1 vs. 2-D-1 vs. 3-A-1 vs. 3-B-1 vs. 3-C-1 vs. 4-A-1)	0/0/0/5/7/0/0/4	1/1/1/7/0/10/1/0	26.035	0.001
P_4*				
3 vs. 4 canals (M + D) [3-B vs. 4-A]	5/8	4/10	0.805	0.669
Discrete types (1-A-1 vs. 2-C-1 vs. 2-D-1 vs. 3-B-1 vs. 3-C-1 vs. 4-A-1)	1/1/2/5/1/8	0/1/2/4/0/10	2.307	0.805

Note: shaded indicates significant *p*-value; *inter-specific P_4 root number variation was low and not tested for (i.e., C-shaped vs. two roots).

TABLE 4. Bifid apex frequency for double rooted mandibular premolars

Root Type	2-C-1	3-A-1	3-B-1	4-A-1
P_3				
A. africanus		83% D		66% D
P. robustus			100% D	
Gorilla[1]		82% D		
Pongo[1]		62% D		100% B
P_4				
A. africanus	0%		20% D	85% (57% D, 28% B)
P. robustus	100% D		75% D	75% (50% D, 25% B)
Gorilla[1]	26% D		75% (58% D, 17% B)	100% (40% D, 60% B)
Pongo[1]	20% D		89% D	100% B

Note: frequency indicates percentage of measureable specimens; D–distal root, B–both roots; 1–data from Moore et al., 2015

TABLE 5. CSA (mm^2) for *A. africanus*, *P. robustus* and extant hominoids*

Taxon	Mean	Min	Max	SD	CV	n
		P^3				
A. africanus	63.70	50.40	75.60	8.20	12.90	13
P. robustus	76.20	60.70	95.30	9.50	12.40	17
Pan	42.90	29.90	56.60	5.50	12.90	35
Gorilla	106.70	77.30	142.10	14.80	13.80	46
Pongo[2]	74.80	57.60	111.50	13.10	17.60	27
Hylobates	13.20	9.90	16.50	1.50	11.00	24
		P^4				
A. africanus	72.20	56.20	95.50	12.80	17.70	10
P. robustus	92.50	71.90	115.90	12.50	13.50	22
Pan	38.60	29.90	52.30	6.10	15.80	44
Gorilla	101.20	72.60	125.10	12.30	12.10	43
Pongo[1]	73.50	57.00	97.50	10.10	13.70	29
Hylobates	12.80	9.90	19.70	2.10	16.20	25
		P_3				
A. africanus	64.30	51.70	77.70	7.00	10.80	11
P. robustus	61.60	52.60	80.40	8.10	13.20	13
Pan	45.20	34.80	54.70	4.70	10.40	32
Gorilla	120.40	66.10	178.50	25.10	20.90	40
Pongo	84.10	59.80	133.50	18.30	21.80	26
Hylobates	13.90	9.90	18.20	2.20	15.50	23
		P_4				
A. africanus	74.70	55.70	107.20	13.30	17.80	17
P. robustus	78.50	68.80	94.50	7.00	9.00	14
Pan	43.20	35.00	51.50	4.10	9.40	30
Gorilla	97.70	55.50	124.80	14.80	15.20	43
Pongo[1,2]	77.30	57.60	109.50	12.70	16.50	27
Hylobates	11.40	8.50	15.10	1.50	13.30	24

Note: 1–denotes a non-significant difference from *A. africanus*, 2–denotes a non-significant difference from *P. robustus*; *–data from Moore et al., 2015.

TABLE 6. Intra-specific tests of the ‘size-number continuum’ model on CSA and canal number/root type

Taxon	Group Comparison	Mean Group 1 (n)	SD	Mean Group 2 (n)	SD	U	*p*	Predicted Trend[1]
P^3								
A. africanus	2 vs. 3 canals [2-A vs. 3-A]	63.00 (5)	8.60	64.70 (7)	9.10	14.00	0.639	Yes
P. robustus	2 vs. 3 canals [2-A vs. 3-A]	74.40 (7)	9.60	77.50 (10)	9.70	26.00	0.417	Yes
P^4								
A. africanus	2 vs. 3 canals [2-A vs. 3-A]	63.90 (5)	9.80	80.60 (5)	9.90	3.00	0.047	Yes
P. robustus	2 vs. 3 canals [2-A vs. 3-A]	79.30 (4)	7.30	95.50 (18)	11.50	8.00	0.014	Yes
P_3								
A. africanus	C-shaped (2 canals) vs. 2 roots (3 & 4 canals) [2-D vs. 3-A/4-A]	63.90 (3)	7.00	64.40 (8)	7.40	9.00	0.630	Yes*
P. robustus	C-shaped (2 canals) vs. 2 roots (3 canals) [2-A/2-D vs. 3-B]	60.00 (7)	6.30	60.00 (4)	7.90	13.00	0.927	No*
A. africanus	2 roots w/ 3 vs. 4 canals [3-A vs. 4-A]	63.90 (4)	7.00	61.80 (4)	7.10	7.00	0.886	No
P_4								
P. robustus	C/Ɔ-shaped (2 canals) vs. 2 roots (3 & 4 canals) [2-D vs. 3-B/4-A]	75.50 (2)	0.70	79.60 (11)	7.60	7.00	0.513	Yes
A. africanus	2 roots w/ 3 vs. 4 canals [3-B vs. 4-A]	76.40 (5)	18.30	79.10 (8)	8.70	14.00	0.435	Yes
P. robustus	2 roots w/ 3 vs. 4 canals [3-B vs. 4-A]	76.10 (4)	4.90	81.50 (7)	8.40	9.00	0.412	Yes

Note: 1–in all cases the predicted trend is that premolars with greater numbers of canals/roots will exhibit larger CSA. For example, double vs. triple canal P^3/P^4s and double rooted P_3/P_4s w/ two circular vs. single plate-like canals are predicted to display a larger CSA. Shading indicates significant *p*-value;* –indicates <1 mm^2 size difference.

TABLE 7. Summary of inter-specific differences

Character	*A. africanus*	*P. robustus*
Maxillary Premolars		
Single root/canal (1-A-1)	P^3	absent
P^4: typical canal number	2/3	3
Common buccal root groove (2-A-2)	type 2	type 4
P^3 & P^4 tooth size (CSA)	lesser/lesser	greater/greater
Mandibular Premolars		
Single root/canal (1-A-1)	P_4	P_3
P_3: typical canal number	2/3/4	2/3
P_3: typical root form[1]	C-shaped/MB (E) + D (P)/M (P) + D (P)	C-shaped/M (P) + D (P)
C-shaped type with rounded outer face with two circular canals (2-A-3)	absent	P_3
C-shaped type (2-D-1) outer root groove differences	single shallow B concavity	grooves on M + D and sometimes B aspects
Ɔ-shaped type (reverse 2-D-1)	absent	P_4
C-shaped type with 3 canals	P_4	absent
Triple root/canal type (3-C-1)	P_3	P_4
Two canals within two plate-like roots (2-C-1)	absent	P_3
Three canals within two plate-like roots (3-B-1)	P_4	P_3/P_4
Four canals within two plate-like roots (4-A-1)	P_3/P_4	P_4
P_3 & P_4 tooth size (CSA)	greater/lesser	lesser/greater

E–elliptical; P–plate-like

APPENDIX 1. Specimen list with references for taxon and tooth position

Specimen	Taxon	Reference	Premolar	Basis	Reference
MLD 6	*A. africanus*	A	RP^3	1	A
MLD 6	*A. africanus*	A	RP^4	1	A
MLD 9	*A. africanus*	A*	RP^3	1	A
MLD 9	*A. africanus*	A*	RP^4	1	A
MLD 18	*A. africanus*	A	RP_3	1	A
MLD 18	*A. africanus*	A	RP_4	1	A
MLD 27	*A. africanus*	A*	RP_3	2	A
MLD 40	*A. africanus*	A	LP_3	1	A
MLD 40	*A. africanus*	A	LP_4	1	A
MLD 45	*A. africanus*	A	RP^3	1	A
MLD 45	*A. africanus*	A	RP^4	1	A
STS 1	*A. africanus*	B*	LP^3	2	B
STS 5	*A. africanus*	B, J	RP^3	2	J
STS 5	*A. africanus*	B, J	LP^4	2	J
STS 7	*A. africanus*	B*	LP_3	1	B
STS 7	*A. africanus*	B*	LP_4	1	B
STS 12	*A. africanus*	B	LP^3	2	B
STS 12	*A. africanus*	B	LP^4	2	B
STS 17	*A. africanus*	B	LP^3	1	B
STS 17	*A. africanus*	B	LP^4	1	B
STS 30	*A. africanus*	B	RP^4	3	B
STS 36	*A. africanus*	B*	LP_3	1	B
STS 36	*A. africanus*	B*	LP_4	1	B
STS 47	*A. africanus*	B	P^3	3, 5	B
STS 52a	*A. africanus*	H	LP^3	1	H
STS 52a	*A. africanus*	H	LP^4	1	H
STS 52b	*A. africanus*	H	LP_3	1	H
STS 52b	*A. africanus*	H	LP_4	1	H
STS 53	*A. africanus*	B	RP^3	1	B
STS 53	*A. africanus*	B	RP^4	1	B
STS 61	*A. africanus*	B	RP^3	2	B
STS 61	*A. africanus*	B	RP^4	2	B
STS 71	*A. africanus*	B*	RP^3	1	B
STS 71	*A. africanus*	B*	RP^4	1	B
STW 7	*A. africanus*	B	LP_3	3	B
STW 13	*A. africanus*	C	LP^3	1	C
STW 13	*A. africanus*	C	LP^4	1	C
STW 14	*A. africanus*	C*	LP_4	1	C
STW 19a	*A. africanus*	C	RP^3	3	C

STW 39	*A. africanus*	C	LP$_3$	1	C
STW 39	*A. africanus*	C	LP$_4$	1	C
STW 45	*A. africanus*	C	LP^4	3	C
STW 56a	*A. africanus*	C	LP$_4$	3	C
STW 73	*A. africanus*	C	LP^3	1	C
STW 73	*A. africanus*	C	LP^4	1	C
STW 87	*A. africanus*	C	RP$_4$	3	C
STW 95	*A. africanus*	C	LP$_3$	2, 3	C
STW 131	*A. africanus*	C	RP$_3$	2	C
STW 131	*A. africanus*	C	LP$_4$	1	C
STW 142	*A. africanus*	C	RP$_3$	1	C
STW 142	*A. africanus*	C	RP$_4$	1	C
STW 183 (245)	*A. africanus*	C, D*	LP^3	1	C
STW 183 (245)	*A. africanus*	C, D*	LP^4	1	C
STW 193 (194)	*A. africanus*	C	RP$_4$	3	C
STW 212 (240)	*A. Africanus*	C	LP$_3$	3	C
STW 212 (242)	*A. africanus*	C	RP$_4$	3	C
STW 212 (243)	*A. africanus*	C	LP$_4$	3	C
STW 252a (251)	*A. africanus*	T*	LP^3	1	T, C
STW 252i	*A. africanus*	T*	LP^4	3	T, C
STW 280 (282)	*A. africanus*	C	RP^3	3	C
STW 280 (281)	*A. africanus*	C	RP^4	3	C
STW 289	*A. africanus*	C	LP$_3$	1	C
STW 327	*A. africanus*	C	LP$_4$	3	C
STW 384	*A. africanus*	C*	RP$_4$	1	C
STW 391	*A. africanus*	U	RP^3	1	A
STW 391	*A. africanus*	U	RP^4	1	A
STW 401	*A. africanus*	C	RP$_3$	3	C
STW 404	*A. africanus*	C	RP$_3$	1	C
STW 404	*A. africanus*	C	RP$_4$	1	C
STW 498d	*A. africanus*	C*	RP$_3$	1	C
STW 498d	*A. africanus*	C*	RP$_4$	1	C
STW 579	*A. africanus*	D	RP^3	2	A
STW 579	*A. africanus*	D	RP^4	1	A
TM 1511	*A. africanus*	B	LP^3	1	B
TM 1511	*A. africanus*	B	LP^4	1	B
TM 1512	*A. africanus*	B	RP^3	1	B
TM 1512	*A. africanus*	B	RP^4	1	B

DNH 8	*P. robustus*	E	RP$_3$	1	E

DNH 8	*P. robustus*	E	RP_4	1	E
DNH 17	*P. robustus*	F	LP^3	3	F
DNH 19	*P. robustus*	F	LP_4	1	F
DNH 22a	*P. robustus*	F	RP^4	1	F
DNH 27	*P. robustus*	F	LP_4	3	F
DNH 51	*P. robustus*	F	RP_3	1	F
DNH 51	*P. robustus*	F	RP_4	1	F
DNH 58	*P. robustus*	F	LP_3	3	F
DNH 59	*P. robustus*	F	RP^4	3	F
DNH 68	*P. robustus*	F	RP_3	2	F
DNH 68	*P. robustus*	F	RP_4	2	F
SK 6	*P. robustus*	G	LP_3	2	G
SK 6	*P. robustus*	G	LP_4	1	G
SK 7	*P. robustus*	H	RP_4	3	H
SK 11	*P. robustus*	B	RP^3	1	H
SK 11	*P. robustus*	B	LP^4	1	H
SK 12a	*P. robustus*	B	LP^3	1	J
SK 12a	*P. robustus*	B	LP^4	1	J
SK 13.14	*P. robustus*	H	RP^3	1	H
SK 13.14	*P. robustus*	H	RP^4	1	H
SK 18a	*P. robustus*	I	LP_3	3	V
SK 21.21a	*P. robustus*	B	LP^3	1	B
SK 21.21a	*P. robustus*	B	LP^4	1	B
SK 23	*P. robustus*	K	LP_3	1	K
SK 23	*P. robustus*	K	LP_4	1	K
SK 28	*P. robustus*	H	LP^4	3	H
SK 30	*P. robustus*	H	LP_3	3	H
SK 32	*P. robustus*	H	RP^4	3	H
SK 46	*P. robustus*	B	RP^3	1	K
SK 46	*P. robustus*	B	RP^4	1	K
SK 47	*P. robustus*	B, L	RP^4	1	K
SK 48	*P. robustus*	B	RP^3	1	K
SK 48	*P. robustus*	B	RP^4	1	K
SK 49	*P. robustus*	B	RP^3	1	B
SK 49	*P. robustus*	B	RP^4	1	B
SK 52	*P. robustus*	B	RP^3	1	B
SK 52	*P. robustus*	B	RP^4	1	B
SK 55b	*P. robustus*	H	LP_3	1	B
SK 57	*P. robustus*	B	LP^3	1	H
SK 57	*P. robustus*	B	LP^4	1	H

SK 65	*P. robustus*	H	LP^3	1	H
SK 65	*P. robustus*	H	LP^4	1	H
SK 72	*P. robustus*	B	LP_3	3	H
SK 74a	*P. robustus*	J	RP_3	1	J
SK 74a	*P. robustus*	J	RP_4	1	J
SK 74c	*P. robustus*	B	RP^4	3	B
SK 79	*P. robustus*	B	RP^3	1	B
SK 79	*P. robustus*	B	RP^4	1	B
SK 81	*P. robustus*	B	LP_3	1	H
SK 81	*P. robustus*	B	LP_4	1	H
SK 83	*P. robustus*	B	LP^3	1	B
SK 83	*P. robustus*	B	LP^4	1	B
SK 821	*P. robustus*	H	LP^3	3	H
SK 827	*P. robustus*	H	LP_4	3	H
SK 838a	*P. robustus*	B	RP^4	2	H
SK 857	*P. robustus*	H	RP_3	3	H
SK 858.861.883	*P. robustus*	H	LP_3	1	M
SK 876	*P. robustus*	B	RP_3	1	B
SK 876	*P. robustus*	B	RP_4	1	B
SK 1512	*P. robustus*	N	RP^4	1	N
SK 1587a	*P. robustus*	N	LP_3	1	N
SK 1587a	*P. robustus*	N	LP_4	1	N
SK 1588	*P. robustus*	N	RP_3	1	N
SK 1588	*P. robustus*	N	RP_4	1	N
SK 1590a	*P. robustus*	N	RP^4	2	N
SK 1590b	*P. robustus*	N	RP^3	2	N
SK 14001	*P. robustus*	N	LP^3	3	N
SK 14080	*P. robustus*	B	RP^4	2	B
SK 14133	*P. robustus*	O	LP^4	2	O
SKW 5	*P. robustus*	O	RP_3	1	P
SKW 5	*P. robustus*	O	RP_4	1	P
SKW 8	*P. robustus*	O	RP^3	1	O
SKW 8	*P. robustus*	O	RP^4	1	O
SKW 11	*P. robustus*	O	RP^3	1	O
SKW 11	*P. robustus*	O	RP^4	1	O
SKW 12	*P. robustus*	O	LP^3	1	O
SKW 12	*P. robustus*	O	LP^4	1	O
SKW 6113	*P. robustus*	I	RP^3	3	Q
SKX 311	*P. robustus*	O	LP_3	3	O
SKX 3354	*P. robustus*	O	LP^4	3	O

SKX 4446	*P. robustus*	O	RP_3	1	O
SKX 4446	*P. robustus*	O	RP_4	1	O
SKX 50078	*P. robustus*	I	RP^3	3	I
TM 1517a	*P. robustus*	R	LP^3	2	R, S
TM 1517a	*P. robustus*	R	LP^4	2	R, S
TM 1517b	*P. robustus*	R	RP_3	2	R, S
TM 1517b	*P. robustus*	R	RP_4	1	R, S
TM 1600	*P. robustus*	S	LP_3	3	S

References: A–University of the Witwatersrand records; B–Brain, 1981; C–Moggi-Cecchi et al., 2006; D–Lockwood and Tobias, 2002; E–Keyser et al., 2000; F–Moggi-Cecchi et al., 2010; G–Broom, 1949 (originally designated as *P. crassidens*); H–Robinson, 1956; I–Ditsong National Museum of Natural History records; J–Broom and Robinson, 1950; K–Broom and Robinson, 1952; L–Wood and Engleman, 1988; M–Frayer, 1973; N–Brain, 1970; O–Grine, 2004; P–Tobias et al., 1977; Q–de Ruiter, 2001; R–Broom, 1938; S–Thackeray et al., 2001; T–Clarke, 1988; U–Clarke, 2008; V–Robinson, 1953; *–attributed as a different species after Clarke, 1985, 1989, 1994a, 2008; Fornai et al., 2010.

Premolar position basis: 1–*in situ* with all adjacent teeth; 2–*in situ* with some adjacent teeth; 3–based on root morphological features; 4–initial designation adjusted based on overall root morphology; 5–left/right side indeterminate.

APPENDIX 2. Specimen list with element, root type and tooth size (mm^2)

Specimen	P^3	P^4	P_3	P_4
A. africanus				
MLD 6	3-A-5	3-A-5 (71.80)		
MLD 9	2-A-2	2-A-2		
MLD 18			3-A-1 (64.80)	4-A-1 (67.40)
MLD 27			2-D-1	
MLD 40			3-A-1 (62.60)	4-A-1 (70.30)
MLD 45	3-A-5 (67.40)	3-A-5[1]		
STS 1	2-A-2 (70.60)			
STS 5	3-A-5[3]	2-A-2[3]		
STS 7			3-A-1 (68.00)	3-C-1 (77.60)
STS 12	3-A-5 (50.40)	2-A-2		
STS 17	3-A-1 (61.40)	2-A-2 (63.20)		
STS 30		2-A-2 (80.80)		
STS 36			2-D-1 (72.00)	4-A-1 (77.90)
STS 47	1-A-1 (60.40)			
STS 53	2-A-2	2-A-2		
STS 61	2-A-2 (57.20)	2-A-2 (56.20)		
STS 71	3-A-5	2-A-2[1]		
STW 7			2-D-1 (59.20)	
STW 13	3-A-5 (66.50)	3-A-5 (76.90)		
STW 14				4-A-1 (71.80)
STW 19a	2-A-2[1]			
STW 39			3-A-1[1]	2-C-1 (56.10)
STW 45		3-A-5 (73.30)		
STS 52a	2-A-2	2-A-2		
STS 52b			3-A-1	2-D-1
STW 56a				4-A-1 (89.60)
STW 73	2-A-2 (55.70)	2-A-2 (60.60)		
STW 87				1-A-1 (55.70)
STW 95			2-D-1 (60.60)	
STW 131			3-A-1	3-B-1 (73.40)
STW 142			4-A-1 (60.60)	3-B-1 (64.90)
STW 183 (STW 245)	2-A-2 (74.10)[1]	2-A-2[3]		
STW 193 (STW 194)				4-A-1 (85.20)
STW 212 (STW 240)			4-A-1 (62.10)	
STW 212 (STW 242)				3-B-1 (75.70)
STW 212 (STW 243)				2-D-1 (66.30)*
STW 252a	3-A-5 (75.60)			
STW 252i		3-A-5 (95.90)		
STW 280 (STW 281)		3-A-5 (85.30)[1]		
STW 280 (STW 282)	3-A-5 (74.50)			

STW 289			2-D-1	
STW 327				4-A-1 (80.60)[4]
STW 384				3-B-1 (107.20)
STW 391	2-A-2	3-A-1		
STW 401			4-A-1 (77.70)	
STW 404			3-A-1 (51.70)	3-B-1 (60.70)
STW 498d			4-A-1 (67.60)	4-A-1 (89.90)
STW 579	3-A-5[1]	3-A-5		
TM 1511	3-A-5 (57.30)	2-A-2 (58.70)		
TM 1512	2-A-2 (57.70)	2-A-2[3]		
P. robustus				
DNH 8			3-B-1 (66.50)	4-A-1 (84.10)
DNH 17	2-A-2			
DNH 19				4-A-1 (94.50)
DNH 22a		3-A-5 (72.80)		
DNH 27				4-A-1 (71.70)
DNH 51			(60.70)[2]	3-B-1 (78.20)
DNH 58			1-A-1	
DNH 59		2-A-2 (74.80)		
DNH 68			2-D-1 (66.60)	4-A-1
SK 6			2-D-1 (65.40)	3-B-1 (79.50)
SK 7				4-A-1 (83.30)
SK 11	2-A-2 (71.30)	2-A-2 (87.90)		
SK 12a	3-A-5 (95.30)	3-A-5 (115.90)		
SK 13.14	2-A-2 (68.50)	3-A-5 (95.60)		
SK 18a			2-D-1 (53.00)	
SK 21.21a	3-A-5	3-A-5		
SK 23			3-B-1 (52.60)	4-A-1 (73.30)
SK 28		3-A-2 (97.26)		
SK 30			2-D-1 (60.70)	
SK 32		3-A-5 (90.00)		
SK 46	3-A-5 (71.40)	3-A-1 (89.60)		
SK 47		2-A-2 (82.50)		
SK 48	3-A-5 (74.60)	3-A-5		
SK 49	3-A-5	3-A-5 (112.90)		
SK 52	3-A-5 (88.80)	3-A-5 (104.30)		
SK 55b			3-B-1[4]	
SK 57	3-A-5 (81.60)	3-A-5 (106.90)		
SK 65	3-A-5 (79.40)	3-A-5 (101.60)		
SK 72			3-B-1 (67.00)	
SK 74a			2-D-1 (52.80)	2-D-1 (75.00)
SK 74c		3-A-5 (100.10)		
SK 79	3-A-1	3-A-5 (80.40)		

SK 81			2-D-1	4-A-1 (88.30)
SK 83	2-A-2 (77.20)	3-A-5 (102.20)		
SK 821	3-A-5 (75.40)			
SK 827				3-B-1 (68.80)[1]
SK 838a		3-A-5 (80.40)		
SK 857			2-D-1 (65.20)	
SK 858.861.883			3-B-1	
SK 876			3-B-1	4-A-1
SK 1512		3-A-5		
SK 1587a			3-C-1	2-C-1 (72.50)
SK 1588			3-B-1	3-B-1 (77.80)
SK 1590a		2-A-2 (71.90)		
SK 1590b	2-A-2 (60.70)			
SK 14001	2-A-2 (73.50)			
SK 14080		3-A-5		
SK 14133		3-A-5[1]		
SKW 5			3-B-1 (53.80)	4-A-1 (75.50)
SKW 8	3-A-5	3-A-5 (92.90)		
SKW 11	3-A-5 (77.90)	3-A-5 (100.40)		
SKW 12	3-A-5 (61.30)	3-A-5 (83.80)		
SKW 6113	2-A-2 (91.60)			
SKX 311			2-A-3 (56.00)	
SKX 3354		3-A-5		
SKX 4446			3-B-1	2-D-1 (76.00)**
SKX 50078	2-A-2 (78.10)			
TM 1517a	3-A-5 (69.10)	3-A-5 (91.90)		
TM 1517b			3-B-1	4-A-1
TM 1600			2-C-1 (80.40)	

Note: Blank CSA value indicates unmeasurable cervix; *C-shaped type with 3 canals; **Ↄ-shaped type; 1–missing root structure, enough anatomy present for scoring ; 2–damaged root structure precludes scoring, but not CSA measurement; 3–missing tooth or matrix filled alveolus, scoring inferred from other specimens; 4–slightly incomplete canal growth, scoring inferred from other specimens.

APPENDIX 3. Maxillary premolar root type and CSA (mm^2)

Canals	1	2		3	3	3	
Roots	1	2		2	2	3	
Root Type	1-A-1**	2-A-2	SD	3-A-1**	3-A-2**	3-A-5	SD
P^3							
A. africanus	60.40 (1)	63.00 (5)	8.60	61.40 (1)		65.30 (6)	9.80
P. robustus		74.40 (7)	9.60	*		77.50 (10)	9.70
P^4							
A. africanus		63.90 (5)	9.80	*		80.60 (5)	9.90
P. robustus		79.30 (4)	7.30	89.60 (1)	97.30 (1)	95.70 (16)	12.20

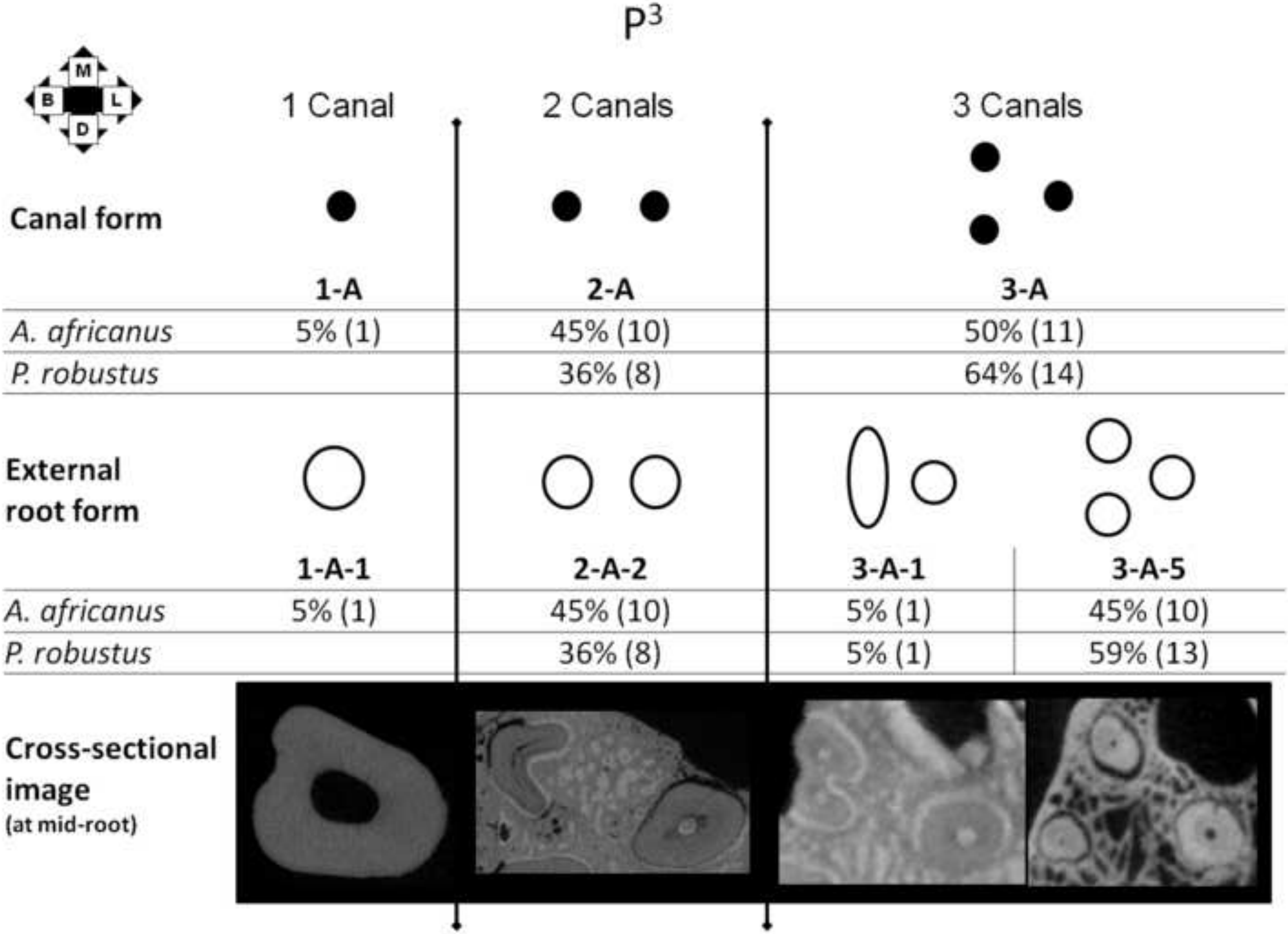
Note: specimen number in brackets; *specimen damaged, measurement not possible; **SD could not be calculated, n=1.

APPENDIX 4. Mandibular premolar root type and CSA (mm^2)

Canals	1	2	2	2		3		3		3	4	
Roots	1	1	2	1		2		2		3	2	
Root Type	1-A-1**	2-A-3**	2-C-1**	2-D-1	SD	3-A-1	SD	3-B-1	SD	3-C-1**	4-A-1	SD
P_3												
A. africanus				63.90 (3)	7.00	61.80 (4)	7.10				67.00 (4)	7.70
P. robustus	*	56.00 (1)	80.40 (1)	60.60 (6)	6.30			60.00 (4)	7.90	*		
P_4												
A. africanus	55.70 (1)		58.40 (1)	66.30 (1)	**			76.40 (5)	18.30	77.620 (1)	79.10 (8)	8.70
P. robustus			76.60 (1)	75.50 (2)	0.70			76.10 (4)	4.90		81.50 (7)	8.40

Note: specimen number in brackets; *specimen damaged, measurement not possible; **SD could not be calculated, n=1.

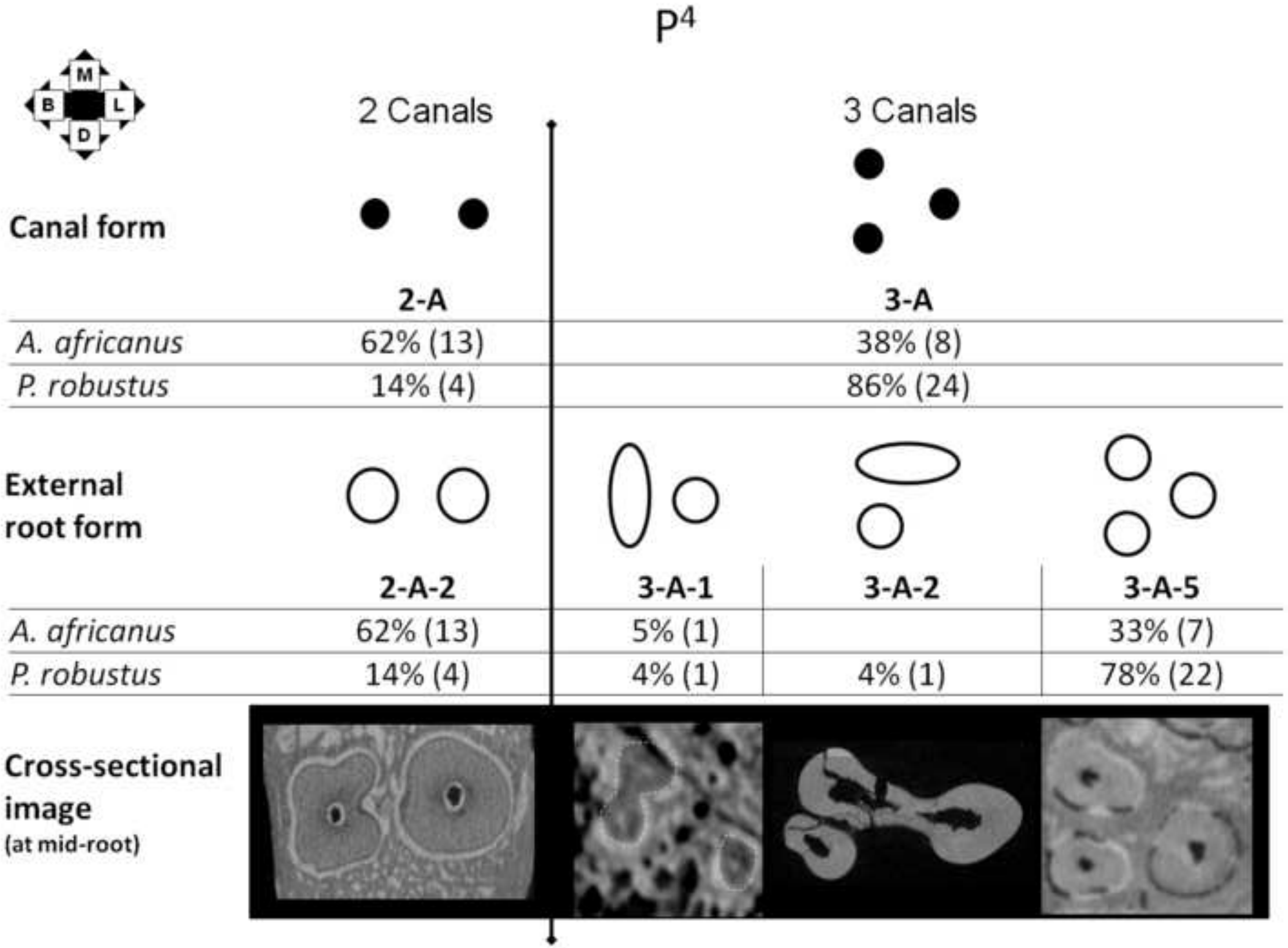
Figure 1



Canal form	1-A	2-A	3-A
A. africanus	5% (1)	45% (10)	50% (11)
P. robustus		36% (8)	64% (14)

External root form	1-A-1	2-A-2	3-A-1	3-A-5
A. africanus	5% (1)	45% (10)	5% (1)	45% (10)
P. robustus		36% (8)	5% (1)	59% (13)

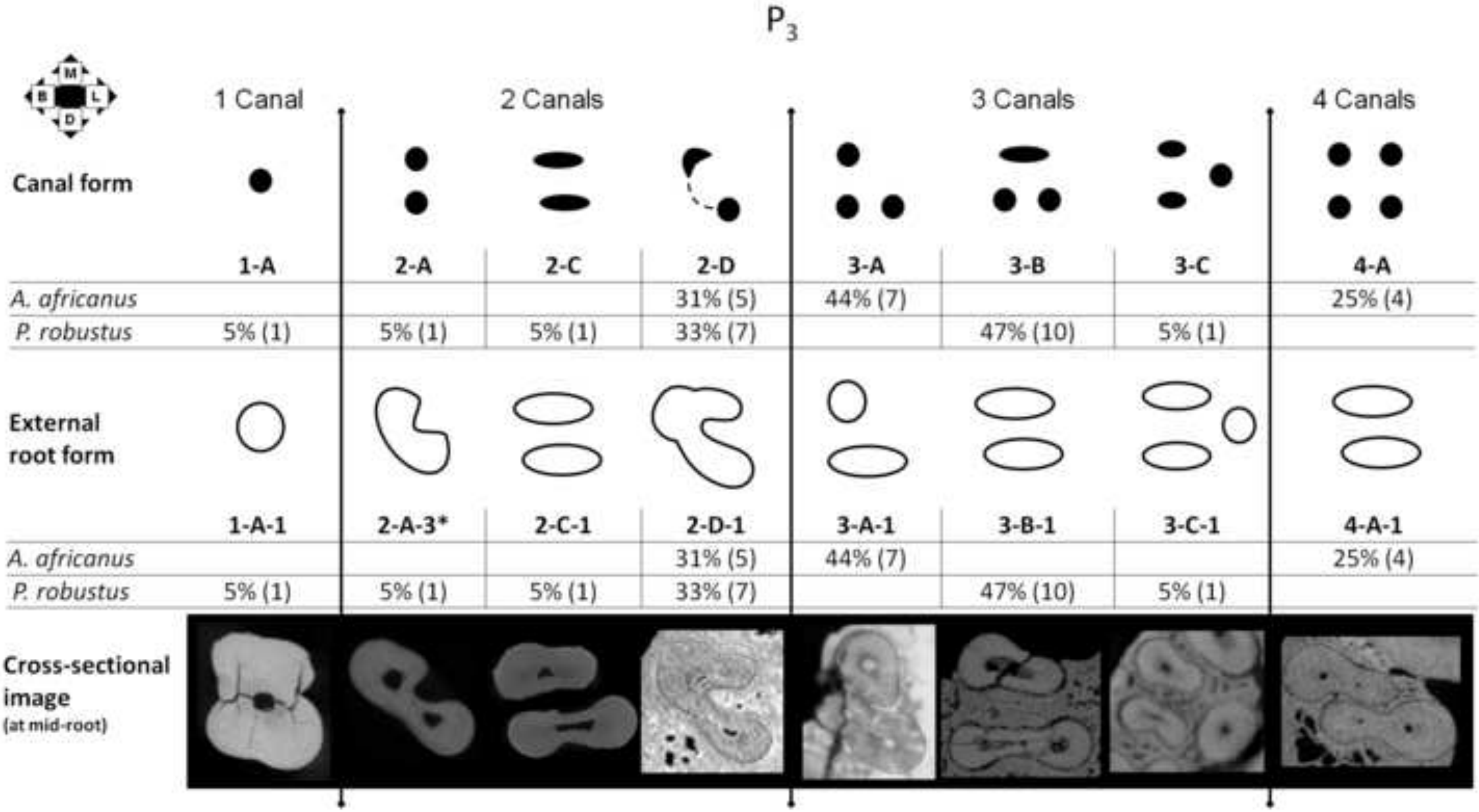
Figure 2



Canal form	2-A	3-A
A. africanus	62% (13)	38% (8)
P. robustus	14% (4)	86% (24)

External root form	2-A-2	3-A-1	3-A-2	3-A-5
A. africanus	62% (13)	5% (1)		33% (7)
P. robustus	14% (4)	4% (1)	4% (1)	78% (22)

Figure 3



Canal form	1-A	2-A	2-C	2-D	3-A	3-B	3-C	4-A
A. africanus				31% (5)	44% (7)			25% (4)
P. robustus	5% (1)	5% (1)	5% (1)	33% (7)		47% (10)	5% (1)	

External root form	1-A-1	2-A-3*	2-C-1	2-D-1	3-A-1	3-B-1	3-C-1	4-A-1
A. africanus				31% (5)	44% (7)			25% (4)
P. robustus	5% (1)	5% (1)	5% (1)	33% (7)		47% (10)	5% (1)	

Figure 4

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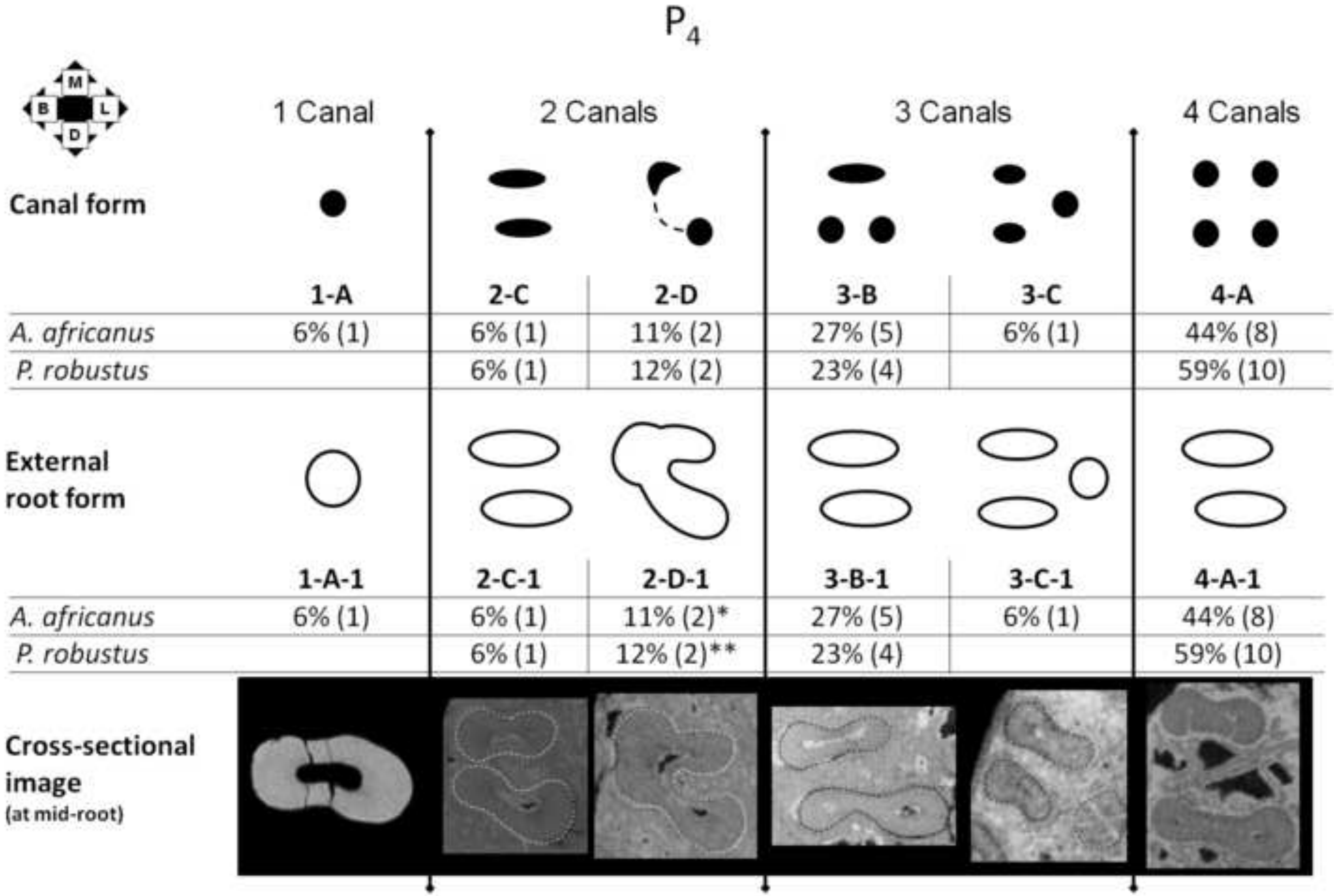


	1-A	2-C	2-D	3-B	3-C	4-A
A. africanus	6% (1)	6% (1)	11% (2)	27% (5)	6% (1)	44% (8)
P. robustus		6% (1)	12% (2)	23% (4)		59% (10)

	1-A-1	2-C-1	2-D-1	3-B-1	3-C-1	4-A-1
A. africanus	6% (1)	6% (1)	11% (2)*	27% (5)	6% (1)	44% (8)
P. robustus		6% (1)	12% (2)**	23% (4)		59% (10)

Figure 5

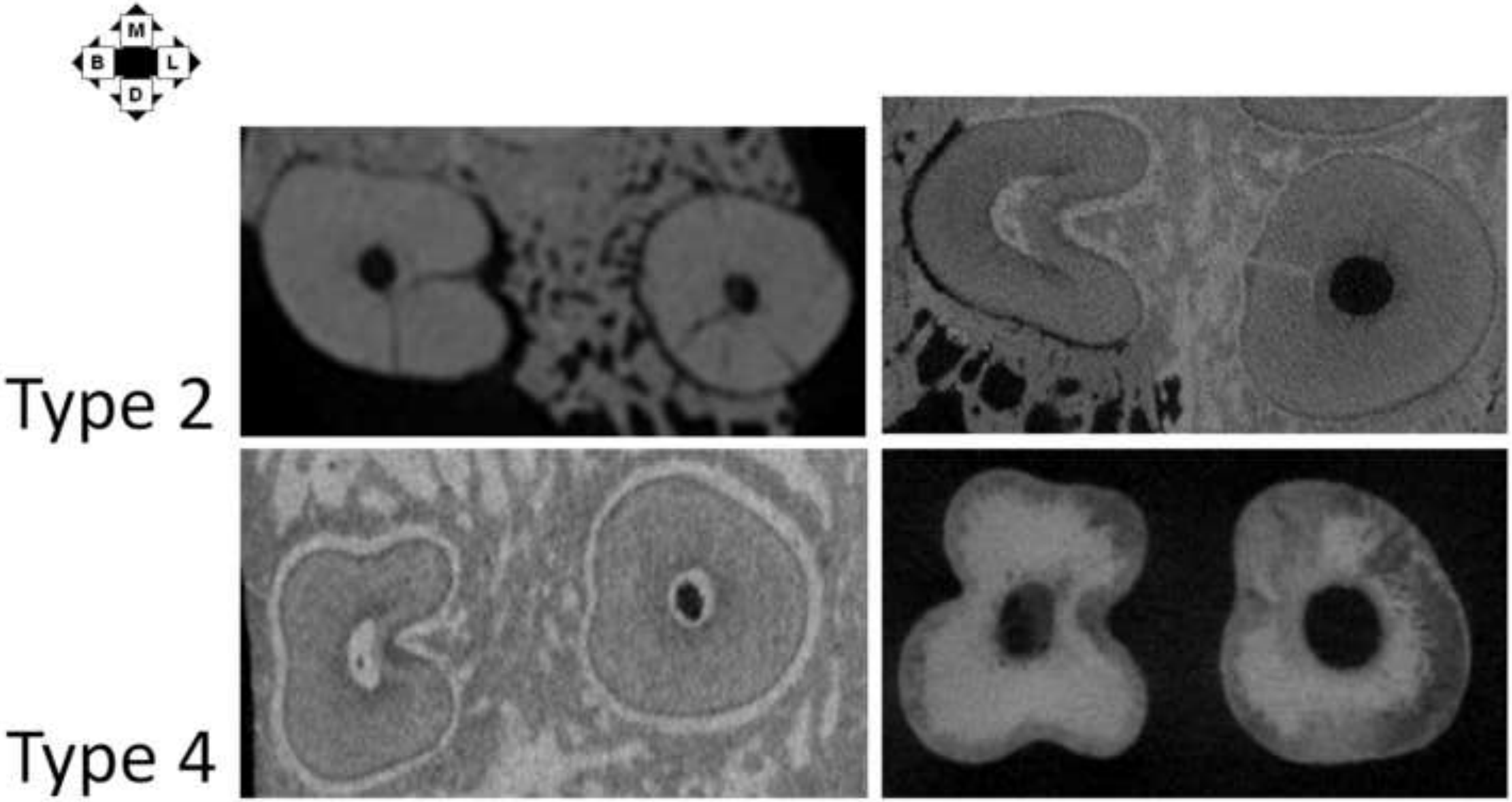


Figure 6

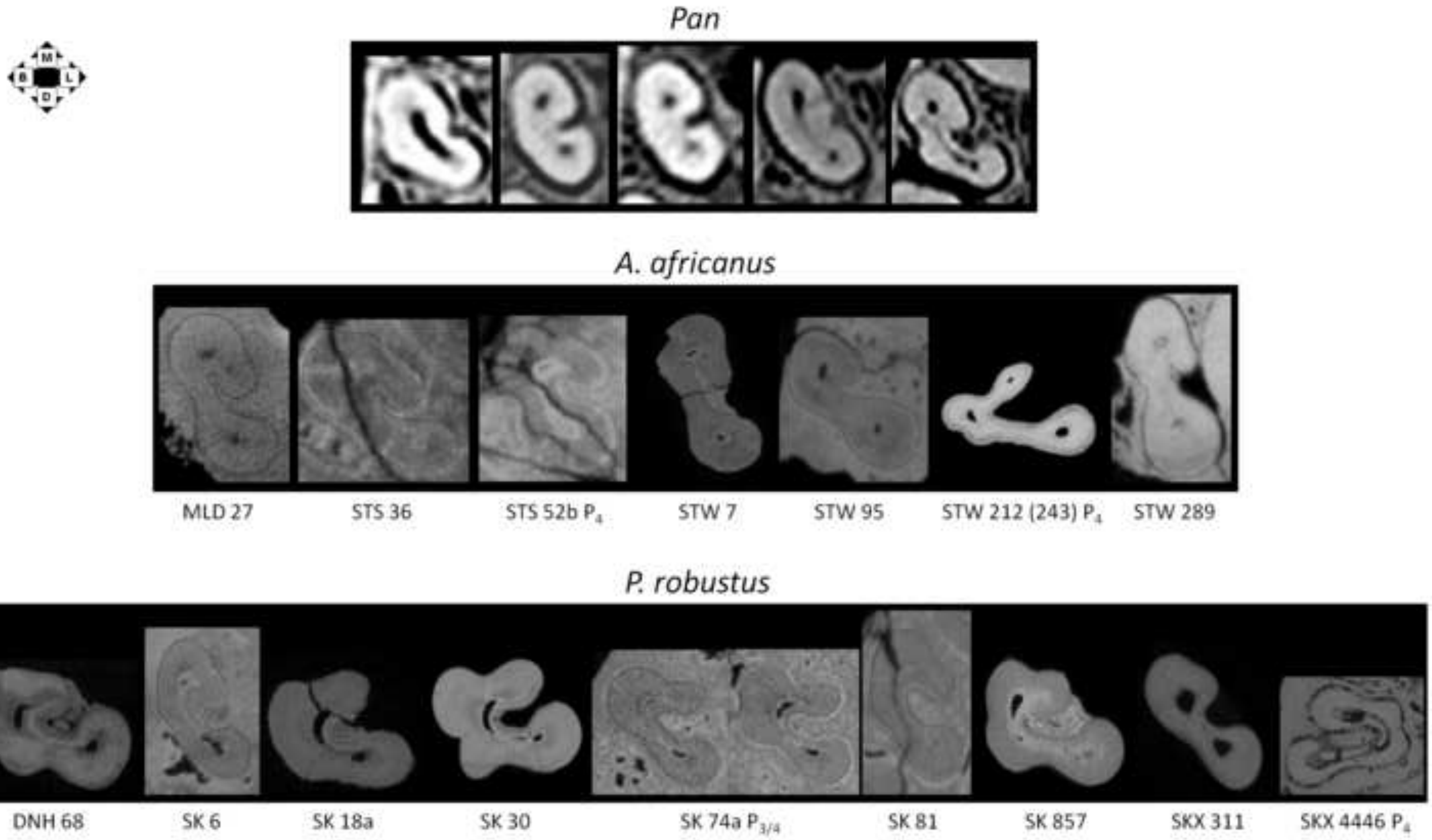

M
B
L
D
Pan
A. africanus
MLD 27
STS 36
STS 52b P4
STW 7
STW 95
STW 212 (243) P4
STW 289
P. robustus
DNH 68
SK 6
SK 18a
SK 30
SK 74a P3/4
SK 81
SK 857
SKX 311
SKX 4446 P4

Figure 7

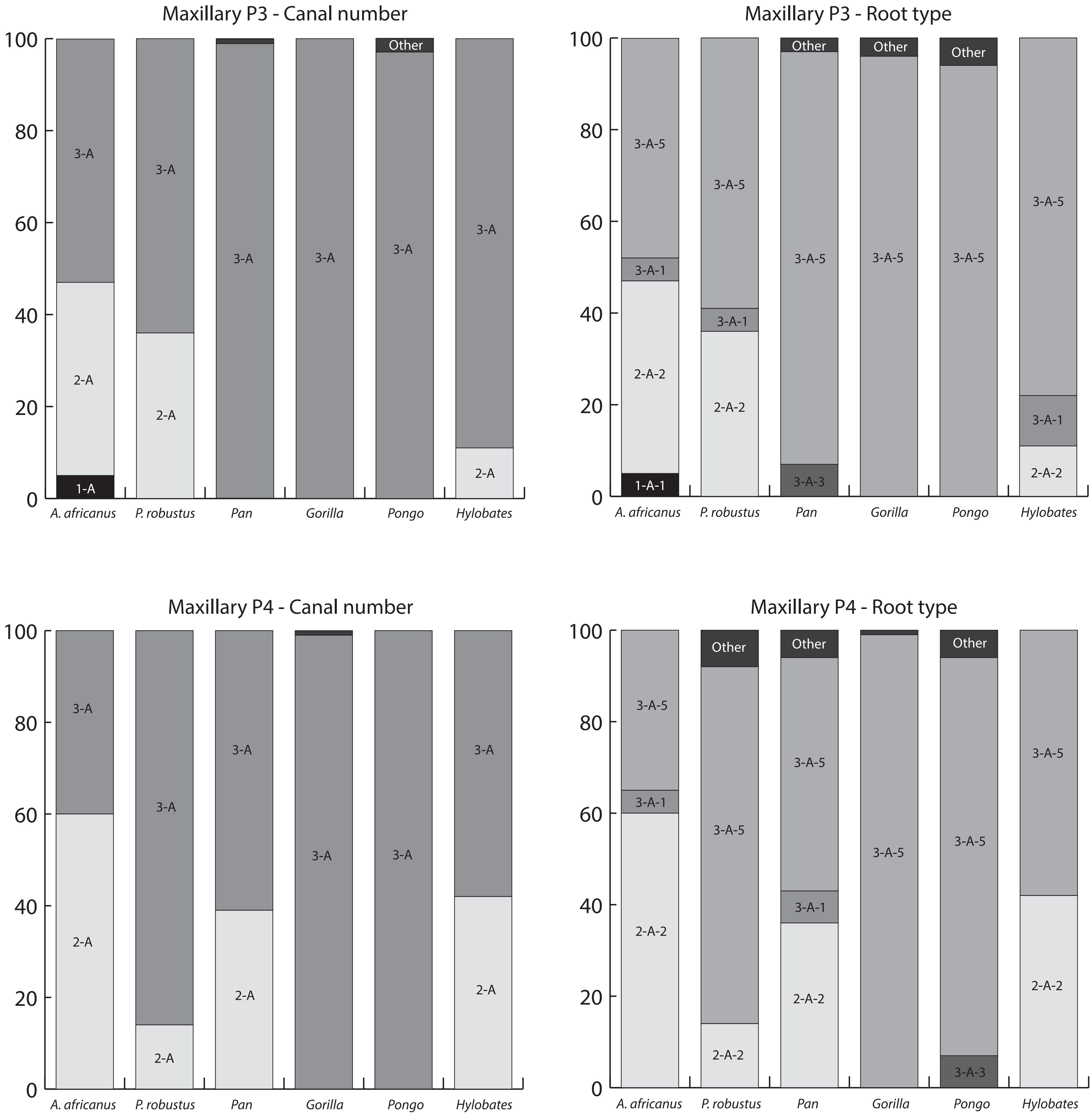
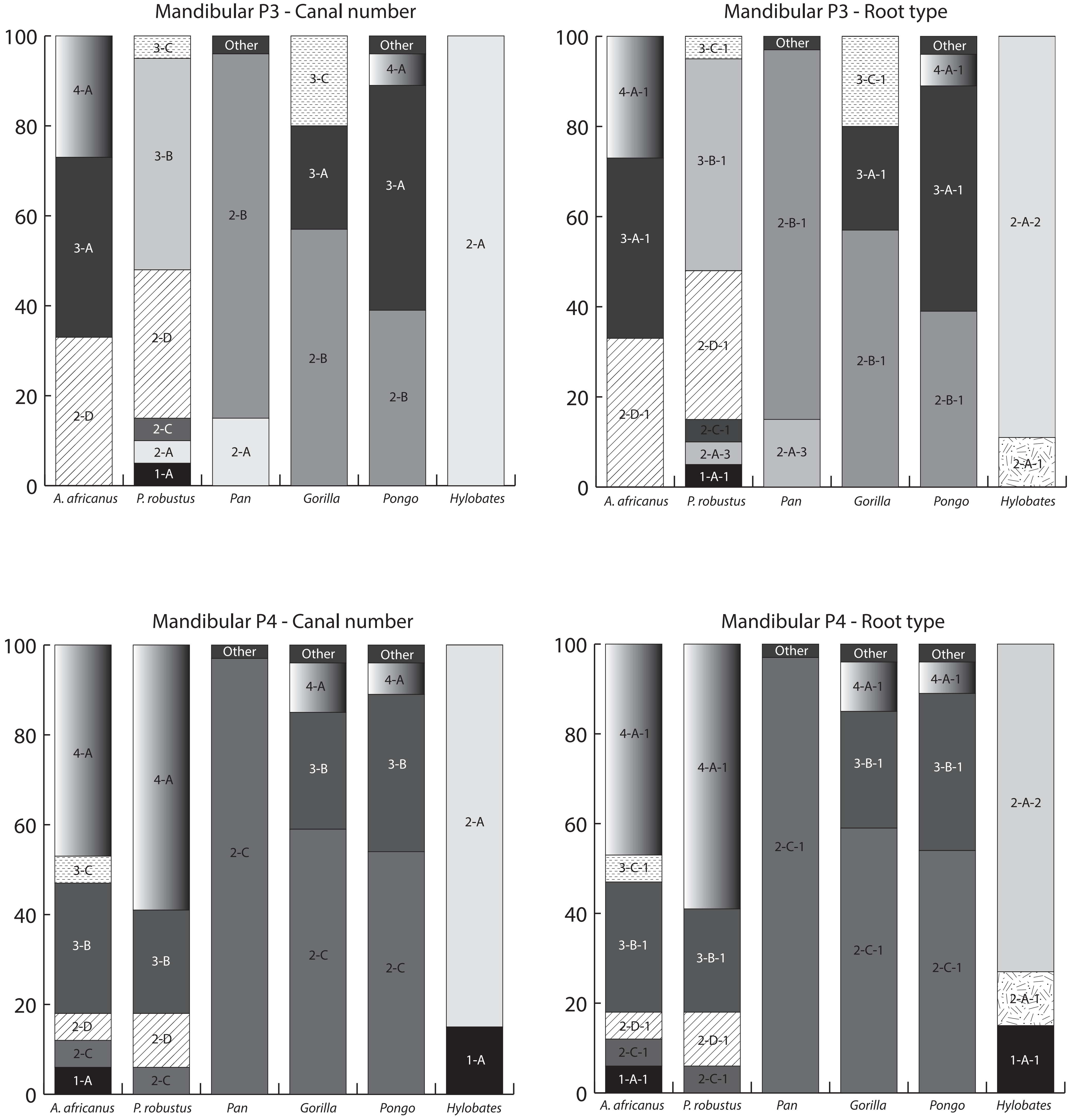

Maxillary P3 - Canal number
100
80
60
40
20
0
3-A
2-A
1-A
A. africanus
P. robustus
Pan
Gorilla
Pongo
Hylobates
Other
Maxillary P3 - Root type
3-A-5
3-A-1
2-A-2
1-A-1
3-A-3
2-A-2
Maxillary P4 - Canal number
Maxillary P4 - Root type

Figure 8


Mandibular P3 - Canal number

Mandibular P3 - Root type

Mandibular P4 - Canal number

Mandibular P4 - Root type