Current Trends in Dental Morphology Research

PREMOLAR ROOT NUMBER VARIATION IN HOMINOIDS: GENETIC POLYMORPHISM VS. FUNCTIONAL SIGNIFICANCE

KORNELIUS KUPCZIK[1,2*], FRED SPOOR[2], ANDREAS POMMERT[3], M. CHRISTOPHER DEAN[2]

[1]*Department of Biology and Hull York Medical School, University of York, York YO10 5DD, UK;* [2]*Department of Anatomy & Developmental Biology, UCL, London, WC1E 6BT, UK;* [3]*Institute of Medical Informatics, University Hospital Eppendorf, 20246 Hamburg, Germany*

ABSTRACT

Premolars are the tooth group with the largest variation in tooth root number and form among extant and extinct primates. Yet it remains unclear whether the range in premolar root number from one to three simply reflects genetic polymorphism or whether variation in root number is an adaptation to dietary specialisation. It has been shown that differences in occlusal loading in primates are strongly linked to differences in root attachment area. Teeth that are subjected to relatively larger masticatory stress should hence bear larger roots. Here we address the question whether there is empirical evidence to support the hypothesis that an increase in premolar root number is a mechanism to increase root attachment area. Then, we describe the relationship between occlusal crown area and root surface area and ask to what extent crown area and concomitant root expansion and root length co-vary and/or combine to influence root surface area in premolars with different root numbers.

High-resolution CT-scans were made of the mandibular and maxillary dentitions of four *Pan troglodytes,* two *Gorilla gorilla*, two *Pongo pygmaeus* and two *Homo sapiens* skulls together with 40 extracted human premolars. Three-dimensional imaging software was used to visualise the teeth and quantify root surface area, occlusal crown area and root length in order to establish any relationship between these parameters in single and multi-rooted premolars.

Root attachment area is found to be not significantly different between maxillary and mandibular premolar pairs. Irrespective of root number, root surface area increases as crown area increases. When root surface area was scaled against root length, the slopes of the RMA

---

[*] Correspondence to: Dr Kornelius Kupczik, Hull York Medical School, University of York, York YO10 5DD, United Kingdom; e-mail: kornelius.kupczik@hyms.ac.uk

regressions indicate that a single-rooted premolar gains less root surface area than a multi-rooted premolar of the same length. Furthermore, single-rooted premolars gain root attachment area either from an enlarged root girth, a consequence of an increase in crown size, or from an independent lengthening of the root. On the other hand, multi-rooted premolars achieve increased attachment area by a combined increase in girth and root length where both these factors are associated with enlarged crown area.

These findings show that an increase in premolar root number is not necessarily related to an increase in root surface area and that root number alone does not then reflect a functional adaptation related to area of root attachment. We suggest that premolar root number variation among hominoids may primarily constitute a genetic polymorphism which may be a good reflection of phylogeny. However, multiple roots do have a clear functional advantage when root length is constrained: for a given increase in root length they gain substantially more in attachment area than single-rooted premolars. Moreover, multiple roots can spread in different directions and better sustain occlusal loads during different phases of the chewing cycle.

INTRODUCTION

Premolar teeth in both extant and extinct primates are more variable in their root morphology than any other the tooth type (Bennejeant, 1936; Senyürek, 1953; Goh, 1957; Remane, 1960; Turner, 1981; Abbott, 1984; Wood et al., 1988; Tobias, 1995). A number of studies of fossil hominins have demonstrated that both mandibular and maxillary premolar root form and number emerge as useful taxonomic indicators (Ward et al., 1982; Abbott, 1984; Wood and Engleman, 1988; Wood et al., 1988; Tobias, 1995; Bermúdez de Castro et al., 1999; White et al., 2000; Haile-Selassie, 2001; Brunet et al., 2002; Leakey et al., 2001). Several premolar root configurations have been identified, either on the basis of external morphology (Abbott, 1984; Wood and Engleman, 1988; Wood et al., 1988) or number of root canals alone (Tobias, 1995). The plesiomorphic condition, where mandibular premolars bear two roots and maxillary premolars three, is found in great apes, while modern humans generally show an apomorphic condition of single rooted premolars, but more often than not with a double-rooted or bifurcated P^3. Variation in premolar root number more than likely represents a genetic polymorphism (Tobias, 1995), but might also be an adaptation to food processing strategy and diet. For instance, it has been demonstrated that differences in dietary specialisations among primates are strongly linked to differences in root attachment area (Kupczik, 2003; Spencer, 2003). Teeth with greater root attachment areas seem likely to sustain higher occlusal forces than teeth with smaller attachment areas. This increase in area can potentially be achieved by either lengthening and widening the roots or by increasing root number from one to two or from two to three. It has also been suggested that there is a correlation between increased root number and enlargement of the crown. Support for this comes from observations among robust australopiths (Sperber, 1974; Tobias, 1995) and other fossil hominins such as *Australopithecus afararensis* and *Ardipithecus ramidus* where premolar root form has even been related to specific features in cuspal morphology (White et al., 2000; Haile-Selassie, 2001). Kovacs (1971) also linked crown with root morphology and noted that modern human teeth with supernumerary roots often have a correspondingly enlarged perimeter at the cervix, an enhanced number of cusps and a larger crown overall.

In this study we present new data for premolar roots in great apes and humans. First, we address the question whether there is empirical evidence to support the hypothesis that an increase in premolar root number is a mechanism to increase root attachment area. Then, we describe the relationship between occlusal crown area and root surface area and ask to what extent crown area and concomitant root expansion and root length co-vary and/or combine to influence root surface area in premolars with different root numbers.

MATERIAL AND METHODS

Transverse computed tomography (CT) scans of skulls were made to include the complete mandibular and maxillary dentitions of four *Pan troglodytes* (two males, two females), two *Gorilla gorilla* (one male, one female), two *Pongo pygmaeus* (two males) and two *Homo sapiens* (males). In addition, 40 extracted human premolars (P_3/P^3 and P_4/P^4) of unknown sex were scanned. The skulls are housed at The Royal College of Surgeons of England, London and the Grant Museum of Zoology and the Department of Anatomy & Developmental Biology of University College London. The human premolars were made available by the Oral Biology Department at The University of Newcastle-upon-Tyne. The skulls and isolated teeth were scanned on a Siemens Somatom Plus 4 using the following parameters: 140 kV, 188 mAs, 1.0 mm slice thickness with a 0.5 mm slice increment and a neutral SP90 convolution filter. Following the data acquisition and a subsequent data processing of the CT datasets, the three dimensional (3D) visualisation and metric analyses of the dental roots was carried out with VOXEL-MAN, a high-resolution volume visualisation system originally developed for medical applications (Höhne et al., 1995; Pommert et al., 2001). The teeth were reconstructed using a threshold based segmentation approach (see Kupczik, 2003 for details). This allowed for the analysis of the gross morphology of the premolars and the quantification of the root surface area, the root length and the occlusal crown area. Root length was measured as the distance between the plane at the cemento-enamel junction and the root tip along the long axis of the root (cf. Abbott, 1984). Occlusal crown area is the product of mesio-distal and bucco-lingual diameters and not only broadly reflects occlusal loads, but is also closely correlated with the girth of the root at the cervix (Hillson et al., 2005). The distinction between two- and three-rooted premolars was made following Abbott (1984). The non-parametric Wilcoxon signed rank test was applied to test for significant differences between maxillary and mandibular premolar tooth root area in the ten specimens with complete dentitions (i.e. P_3s versus P^3s and P_4s versus P^4s, respectively). Moreover, Spearman's rank correlation coefficients (r_s) and reduced major axis (RMA) regression were used to establish the size relationship between the parameters. The significance level of r_s coefficients were determined using t-tests, while the regression slopes were compared using F-tests. Since only the geometric relationships of premolar roots in general irrespective of species differences were of interest here, irrespective of species differences, single and multi-rooted premolars (mandibular and maxillary) of all specimens were pooled. A significance level of $p = 0.05$ was used to reject the null hypothesis for each case.

RESULTS

Figure 1 illustrates the maxillary and mandibular dentition of a male *P. troglodytes* highlighting its premolar root morphology. All great apes except those of three *P. troglodytes* and the female *G. gorilla* exhibit two roots (P_3

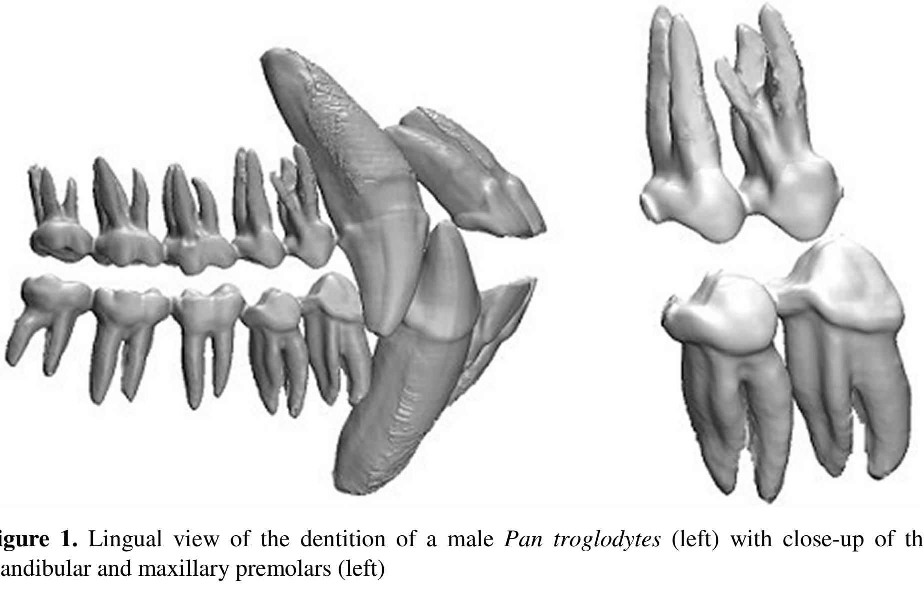

Figure 1. Lingual view of the dentition of a male *Pan troglodytes* (left) with close-up of the mandibular and maxillary premolars (left)

= one mesio-buccal, one distal blade-like root; P_4 = one mesial, one distal blade) in the mandibular and three roots ($P^{3/4}$ = two buccal, one palatal root) in the maxillary premolars (Table 1). The two female *P. troglodytes* possess P_3s with a single root and fused double roots, respectively. One of these specimens and the female *G. gorilla* bear only two roots on the maxillary premolars, whilst one male *P. troglodytes* has a double-rooted P^4. The human premolars have single roots with the exception of two P^3s with two roots (Table 1). Despite unequal root number of P^3 and P_3 and of P^4 and P_4 differences in root surface area for those tooth pairs in the skulls are not significant as was found by using the Wilcoxon signed rank test ($n = 10$, $T = 11$ and 19, respectively, $p > 0.05$).

Table 1. Root number and form in great apes and human mandibular and maxillary premolars. B: buccal; BD: bucco-distal; D: distal; MD: mesio-distal; ML: mesio-lingual; PAL: palatal

Species	P_3	P_4	P^3	P^4
Pan, female 1	2 (1MB; 1D), fused	2 (1M; 1D blades)	2 (1B, 1PAL)	2 (1B, 1PAL)
Pan, female 2	1 (C-shaped)	2 (ML-BD) circular	3 (2B, 1PAL)	2 (1B, 1PAL)
Pan, male 1	2 (1MB, 1D blade)	2 (1M, 1D blades)	3 (2B, 1PAL)	2 (1B, 1PAL)
Pan, male 2	2 (1MB, 1D blade)	2 (1M, 1D blades)	3 (2B, 1PAL)	3 (2B, 1PAL)
Pongo, male 1	2 (1MB, 1D blade)	2 (1M, 1D blades)	3 (2B, 1PAL),	3 (2B, 1PAL)
Pongo, male 2	2 (1MB, 1D blade)	2 (1M, 1D blades)	3 (2B, 1PAL)	3 (2B, 1PAL)
Gorilla, female	2 (1MB, 1D blade)	2 (1M, 1D blades)	3 (2B, 1PAL)	2 (1B, 1PAL)
Gorilla, male	2 (1MB, 1D blade)	2 (1M, 1D blades)	3 (2B, 1PAL)	3 (2B, 1PAL)
Homo, male 1	1 (circular)	1 (circular)	1 (ellipsoid)	1 (ellipsoid)
Homo, male 2	1 (circular)	1 (circular)	2 (1B, 1PAL)	1 (ellipsoid)
Homo, isolated premolars	1 circular to ellipsoid root, n = 10	1 circular to ellipsoid root, n = 10	1 ellipsoid, n = 8 2 (1B-PL) n = 2	1 ellipsoid root, n = 10

Figures 2 to 4 show bivariate plots between premolar root surface area, crown area and root length. Spearman rank correlation and RMA statistics are summarised in Table 2. An enlargement of the crown area correlates with an increase in root surface area that is similar in one-, two- and three-rooted premolars (Figure 2, Table 2). In other words, an increase from a single-rooted to a multi-rooted premolar or from a two-rooted to a three-rooted premolar does not result in a different scaling relationship between crown area and root surface area. In contrast, whilst an increase in root length also correlates well with an increase in root surface area, the scaling pattern of these parameters differs significantly for single and multi-rooted premolars (Figure 3, Table 2). A tooth with multiple roots gains relatively more surface area for a given increase in root length than a single-rooted one. However, there is no difference in RMA slope between premolars with two and three roots (Table 2). Only premolars with multiple roots show a significant correlation between crown area and root length and the RMA slopes are not significantly different (Figure 4, Table 2).

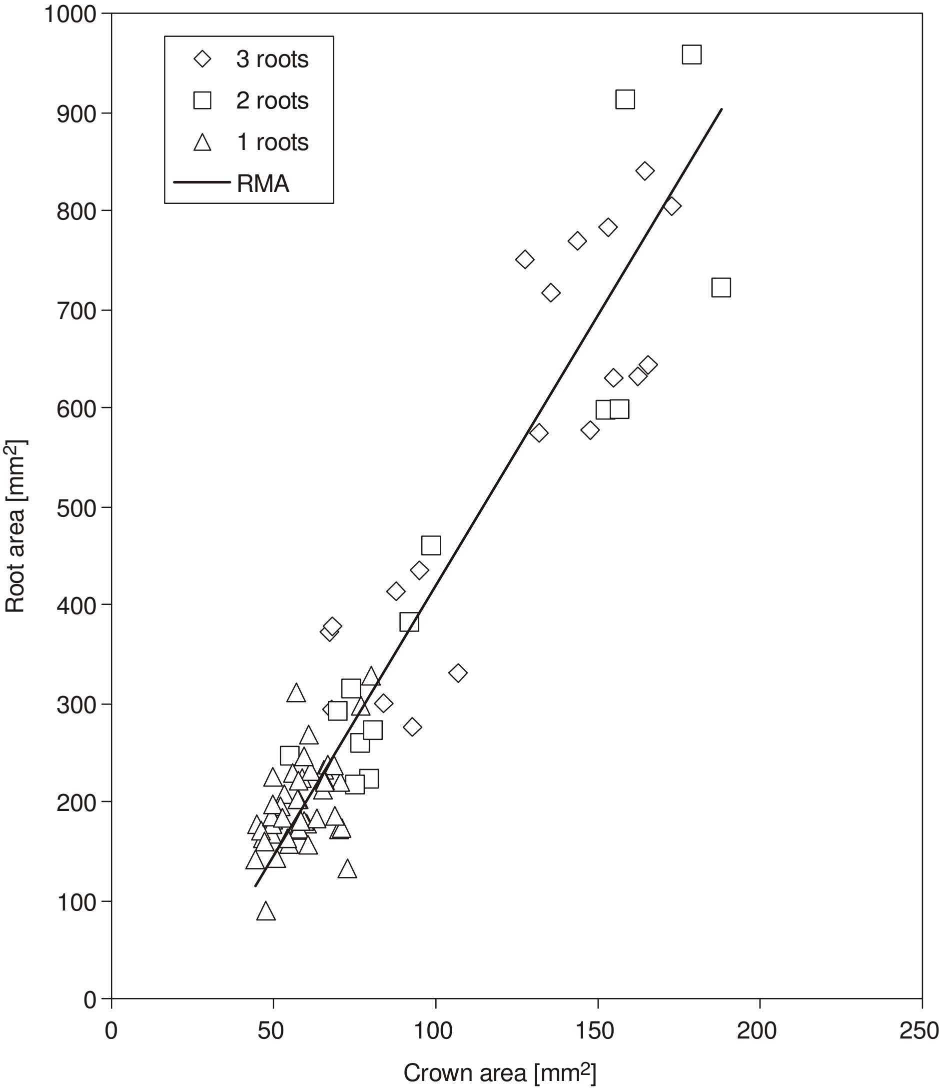

Figure 2. Bivariate plot of the premolar root surface area against occlusal crown area showing RMA regression for the pooled sample

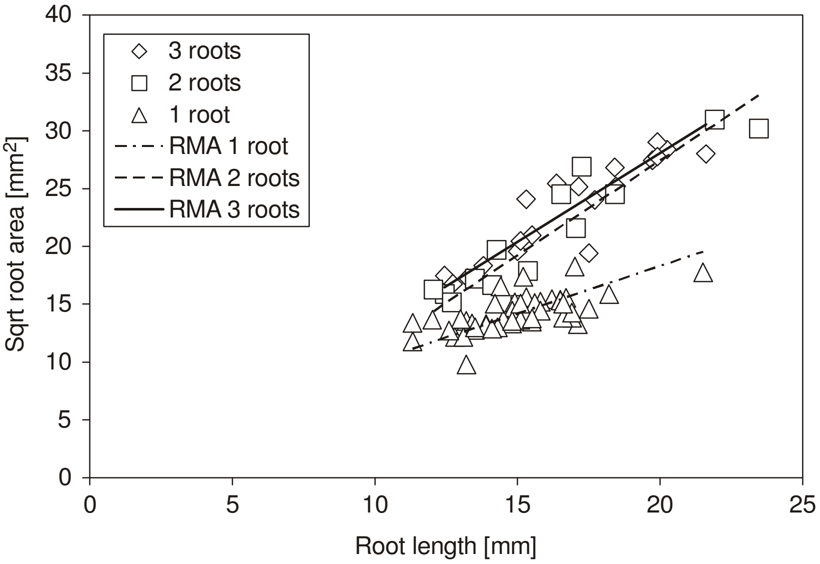

Figure 3. Bivariate plot of premolar root surface area (square rooted) against root length showing RMA regressions

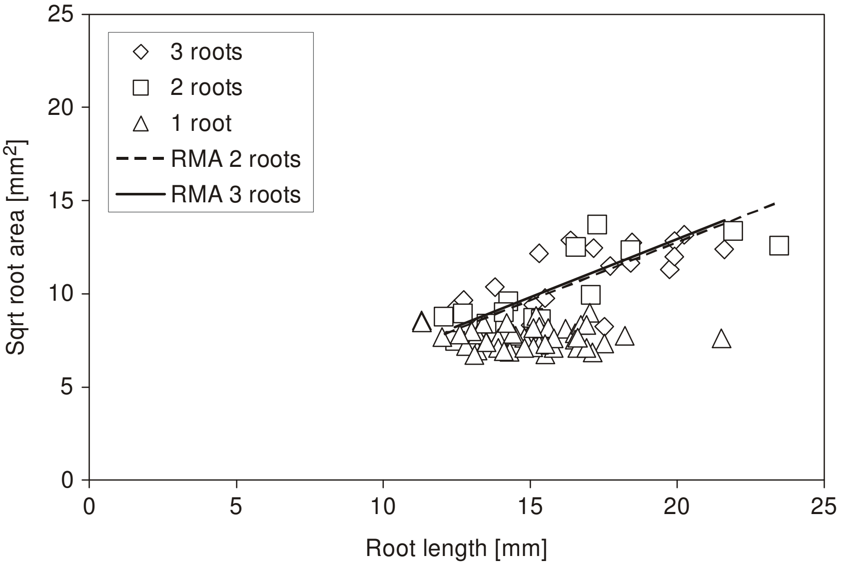

Figure 4. Bivariate plot of premolar crown area (square rooted) against root length showing RMA regressions

Table 2. Spearman rank correlation (r_s) and RMA statistics for premolar root surface area against crown area (A), root surface area (square rooted) against root length (B) and crown area (square rooted) against root length (C). F = F-test probability that slopes between one and two, one and three and two and three rooted premolars are different. **p < 0.01, ***p < 0.001, n.s. = not significantly different

	A	B	C
1 root (n = 47), r_s	0.46**	0.69***	–0.03, n.s.
RMA slope	5.12	0.82	–
95% conf. int.	3.79, 6.45	0.64, 1.01	–
Intercept	–98.62	1.87	–
2 roots (n = 14), r_s	0.84***	0.85***	0.79**
RMA slope	5.53	1.64	0.62
95% conf. int.	4.21, 6.84	1.23, 2.04	0.39, 0.85
Intercept	–143.28	–5.32	0.32
3 roots (n = 19), r_s	0.81***	0.91***	0.67**
RMA slope	5.27	1.54	0.63
95% conf. int.	3.93, 6.60	1.22	0.39, 0.86
Intercept	–90.64	1.86	0.42
F (1 : 2)	n.s.	***	–
F (1 : 3)	n.s.	***	–
F (2 : 3)	n.s.	n.s.	n.s.
1–3 roots (n = 80), r_s	0.85***	0.62***	0.35***
RMA slope	5.47	2.07	0.78
95% conf. int.	5.04, 5.91	1.75, 2.38	0.64, 0.93
Intercept	–126.20	–14.75	–3.31

DISCUSSION

The present study set out to investigate whether an increase in premolar root number is a mechanism to enlarge root attachment area. In addition, we addressed the question that root surface area might be associated with increasing occlusal area and with increase in root length. We then asked if in one, two and three-rooted premolars an increase in root attachment area simply follows on from either an increase root length or from a widening of the roots (that occurs as a consequence of a larger crown), or from both of these potential changes in root morphology.

In this study we followed the definition of root number according to Abbott (1984). This definition bears on our conclusion that no difference in root surface area was found between two-rooted and three-rooted premolars. A tooth with a mesio-buccal root and a blade-like distal root is considered here to be two-rooted. However, the distal portion may be fully "8" shaped in cross-section, with two clearly distinct root canals, and in reality may be better described as having two fused distal roots rather than one. Based on root canals (cf. Tobias, 1995; Ward et al., 1982) such premolars are perhaps better classified as three-rooted. Hence, the strict division between two- and three-rooted specimens is to some extent an artefact of the definition used to classify them, as the findings of this study make clear.

The mandibular and maxillary premolar root morphologies observed in this study are in agreement with previous findings for the three great ape species, and also lend support for the suggestion that *P. troglodytes* females show more variation in root form and number than the males (Abbott, 1984; Wood and Engleman, 1988; Tobias, 1995). A common finding in the dentitions of great apes and humans is that the root number in maxillary premolars is either equal to the number of roots in mandibular premolars or exceeds it by one. Despite these differences in root number between maxillary and mandibular premolar pairs they show similar root attachment areas. Most strikingly however, in the full sample an increase in root attachment area emerges as being directly associated with an increase in crown area (Figure 2), where root number has no effect on root surface area. This is clear evidence to suggest that increasing the number of roots per se does not result in a larger root area which to support of a larger crown with. From this perspective, root number seems less of a biomechanical factor than a genetic polymorphism. However, the way in which a larger root attachment area is achieved clearly differs in the single- and multi-rooted premolars. In single-rooted premolars the increase either comes from the enlarged root girth, a consequence of an increase in crown size, or from an independent lengthening of the root. On the other hand, multi-rooted premolars achieve increased attachment area by a combined increase in girth and root length where both these factors are associated with enlarged crown area (Figures 2 and 4). This difference means that multiple roots have a clear advantage when root length is constrained: for a given increase in root length they gain substantially more in attachment area than single-rooted premolars (Figure 3). Thus, multiple roots can compensate for shorter roots, which are less well adapted to sustain occlusal loads (Levy and Wright, 1978), and thus provide better tooth stability. In fact, this relationship has also been proposed for the P^3s of South African australopiths (Sperber, 1974). A further functional advantage of multiple roots, but not related to attachment area as such, is that they can spread in different directions and better sustain occlusal loads during different phases of the chewing cycle. In this way transverse and oblique forces can be resisted in several directions by the same tooth (Smith, 1986; Macho and Spears, 1999).

It is worth noting that the different scaling relationships observed for single and multi-rooted premolars could follow from factors other than those intrinsically distinguishing these two morphotypes. Nearly all of the single-rooted premolars are modern human and this might reflect an interspecific, non-functional difference between humans and great apes. Moreover, the human sample, with the exception of one skull, derives from an industrial population in which masticatory constraints underlying morphological correlations may have been relaxed (see e.g. Spoor et al., 2005). Nevertheless, the present findings for the single-rooted human premolars in the sample studied here appear to hold true more generally, given that Garn et al. (1978) found only weak correlations between root length and crown diameters of mandibular premolars in a North American sample.

Overall, the results obtained here suggest that in the absence of any constraints on root length, and any advantage conferred by root spread, variation in premolar root number may well constitute a genetic polymorphism linked most closely to phylogenetic differences (Abbott, 1984; Wood et al., 1988; Tobias, 1995). There remains the possibility that variation of root number may, however, be more closely related to cuspal morphology than has been appreciated (Kovacs, 1971). Some support for this comes from observations made by White et al. (2000) regarding the P_3s of the *A. afarensis* specimen MAK-VP-1/12. This specimen is described as combining a well developed mesio-lingual portion of the crown (metaconid) with double-bladed roots as seen in molars. Likewise, the combination of a P_4 with Tomes' root together with a well developed talonid in the Miocene hominin *Ardipithecus ramidus* (Haile-Selassie, 2001) may suggest a potential link between crown and root morphology. Yet another example of this can be found in both the P_3 and P_4 of the *Homo* specimen H1 from Atapuerca. These premolars are characterised by separate disto-lingual and mesio-buccal root components, which are in part mirrored in the crown by an extended talonid (Bermúdez de Castro et al., 1999). Future studies with larger sample sizes that include fossil hominins are likely to shed more light on the issue of multirootedness in premolars.

Acknowledgements

We would like to thank the organisers for all their help and support. We are also grateful to Simon Hillson and Andrew Chamberlain for comments and discussion concerning this project. Thanks also to Karl Heinz Höhne for the use of VOXEL-MAN, Nathan Jeffery for help with the RMA statistics and to Simon Chaplin, Helen Chatterjee and Don Reid for allowing access to specimens and to staff at the Hammersmith Hospital London and London Bridge Hospital London. The authors acknowledge The Leverhulme Trust for funding the CT scans through a grant to MCD.

REFERENCES

Abbott S. A. (1984) *A comparative study of tooth root morphology in the great apes, modern man and early hominids*. PhD thesis, University of London.

Bennejeant C. (1936) *Anomalies et variations dentaires chez les primates*. PhD thesis, Université de Clermont-Ferrand.

Bermúdez de Castro J. M., Rosas A., Nicolás M. E. (1999) Dental remains from Atapuerca-TD6 (Gran Dolina site, Burgos, Spain). *J. Hum. Evol.*, **37**, 523–566.

Brunet M., Guy F., Pilbeam D., Mackaye H. T., Likius A., Ahounta D., Beauvilain A., Blondel C., Bocherens H., Boisserie J. R., De Bonis L., Coppens Y., Dejax J., Denys C., Duringer P., Eisenmann V., Fanone G., Fronty P., Geraads D., Lehmann T., Lihoreau F., Louchart A., Mahamat A., Merceron G., Mouchelin G., Otero O., Pelaez C. P., Ponce de León M. S., Rage J. C., Sapanet M, Schuster M., Sudre J., Tassy P., Valentin X., Vignaud P., Viriot L., Zazzo A., Zollikofer C. (2002) A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, **418**, 145–151.

Garn S. M., Van Alstine W. L., Cole P. E. (1978) Relationship Between Root Lengths and Crown Diameters of Corresponding Teeth. *J. Dent. Res.*, **57**, 636.

Goh S. W. (1957) Variations in the Morphology of Mandibular Premolar Roots. *Brit. Dent. J.*, **102**, 311–314.

Haile-Selassie Y. (2001) Late Miocene hominids from the Middle Awash, Ethiopia. *Nature*, **412**, 178–181.

Hillson S., FitzGerald C., Flinn H. (2005) Alternative Dental Measurements: Proposals and Relationships With Other Measurements. *Am. J. Phys. Anthropol.*, **126**, 418–426.

Höhne K.-H., Pflesser B., Pommert A., Riemer M., Schiemann T., Schubert R., Tiede U. (1996) A new representation of knowledge concerning human anatomy and function. *Nature Medicine*, **1**, 506–511.

Kovacs I. (1971) A Systematic Description of Dental Roots. In *Dental Morphology and Evolution*. A. A. Dahlberg (ed.), Chicago and London: The University of Chicago Press. pp. 211–256.

Kupczik K. (2003) *Tooth root morphology in primates and carnivores*. PhD thesis, University of London.

Leakey M. G., Spoor F., Brown F. H., Gathogo P. N., Kiarie C., Leakey L. N., McDougall I. (2001) New Hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature*, **410**, 433–440.

Levy A. R., Wright W. H. (1978) The Relationship Between Attachment Height and Attachment Area of Teeth Using a Digitizer and a Digital Computer. *J. Periodontol.*, **49**, 483–485.

Macho G. A., Spears I. R. (1999) Effects of Loading on the Biomechanical Behavior of Molars of *Homo*, *Pan*, and *Pongo*. *Am. J. Phys. Anthropol.*, **109**, 211–227.

Pommert A., Höhne K.-H., Pflesser B., Richter E., Riemer M., Schiemann T., Schubert R., Schumacher U., Tiede U. (2001) Creating a high-resolution spatial/symbolic model of the inner organs based on the Visible Human. *Medical Image Analysis*, **5**, 221–228.

Remane A. (1960) Zähne und Gebiß. In *Primatologia. Handbuch der Primatenkunde*. Vol. 3. H. Hofer, A. H. Schultz and D. Starck (eds.), Basel, New York: S. Karger. pp. 637–846.

Senyürek M. S. (1953) A study of the pulp cavities and roots of the lower premolars and molars of Prosimii, Ceboidea and Cercopithecoidea. *Belleten*, **17**, 321–365.

Smith B. H. (1986) Development and Evolution of the Helicoidal Plane of Dental Occlusion. *Am. J. Phys. Anthropol.* **69**, 21–35.

Spencer M. A. (2003) Tooth-Root Form and Function in Platyrrhine Seed-Eaters. *Am. J. Phys. Anthropol.*, **122**, 325–335.

Sperber G. E. (1974) *The morphology of the cheek teeth of early South African hominids*. PhD thesis, University of the Witwatersrand.

Spoor F., Leakey M. G., Leakey L. N. (2005) Correlations of cranial and mandibular prognathism in extant and fossil hominids. *Transactions of the Royal Society of South Africa*. In press.

Tobias P. V. (1995) Root number in the maxillary third premolars: a very ancient polymorphism. In *Aspects of Dental Biology: Palaeontology, Anthropology and Evolution*. J. Moggi-Cecchi (ed.), Florence: International Institute for the Study of Man, pp. 283–290.

Turner II C. G. (1981) Root Number Determination in Maxillary First Premolars for Modern Human Populations. *Am. J. Phys. Anthropol.*, **54**, 59–62.

Ward S. C., Johanson D. C., Coppens Y. (1982) Subocclusal Morphology and Alveolar Process Relationships of Hominid Gnathic Elements From The Hadar Formation: 1974–1977 Collections. *Am. J. Phys. Anthropol.*, **57**, 605–630.

White T. D., Suwa G., Simpson S., Asfaw B. (2000) Jaws and Teeth of *Australopithecus afarensis* From Maka, Middle Awash, Ethiopia. *Am. J. Phys. Anthropol.*, **111**, 45–68.

Wood B. A., Engleman C. A. (1988) Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. *J. Anat.*, **161**, 1–35.

Wood B. A., Abbott S. A., Uytterschaut H. (1988) Analysis of the dental morphology of Plio-Pleistocene hominids. IV. Mandibular postcanine root morphology. *J. Anat.*, **156**, 107–139.