Tooth Size and Shape and their Relevance to Studies of Hominid Evolution [and Discussion]

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Tooth size and shape and their relevance to studies of hominid evolution

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Teeth have the potential to provide evidence about both the patterns of diversity of fossil hominids and the functional adaptations of early hominid taxa. Comparative studies of dental function and the direct examination of wear patterns in fossil teeth are now providing data for testing hypotheses that major differences in dietary adaptations underlie lineage diversity in the early hominids.

However, this review focuses on the contributions that dental evidence can make to hominid systematic studies. Attention is drawn to the value of tooth enamel as a morphological marker and the major contribution that teeth make to the hominid fossil sample. Systematic analysis of hominid remains must start with the identification of patterns of morphological variation. Only then can the taxonomic significance of the morphological differences be assessed and attempts made to link designated taxa in a phylogenetic scheme. The preliminary results of a detailed metrical survey of early hominid premolar and molar teeth are presented. As part of this study cusp areas of first mandibular molars were measured by planimetry. Analysis of these data, without any prior assumptions about taxonomic groups, has demonstrated that the major axis of variation separates the pooled sample into morphological subgroups. These methods provide a systematic and rigorous way of identifying patterns of tooth crown morphology and will allow a more objective assessment of the affinities of individual specimens. Fossil taxa are described in terms of both absolute and relative tooth size. If canine base area and molar crown area are considered there is considerable overlap between *Australopithecus africanus* and *Australopithecus* (*Paranthropus*) *robustus* whereas there is little or no overlap between the ranges of *Australopithecus africanus* and *Australopithecus* (*Paranthropus*) *boisei*. Differences in relative tooth size among fossil taxa are taken as an example of how to attack the problem of assessing the taxonomic significance of morphological differences. Analogues from modern primates are used to derive tooth–body size relations for three relative growth models. The results suggest that increases in body size are usually accompanied by a more rapid rate of increase in canine size than in molar size. This suggests that the relatively smaller canines of the ‘robust’ australopithecines are not the result of simple scaling, but represent the result of selection against an allometric trend. Preliminary results of a survey of the subocclusal morphology of fossil teeth are presented to indicate the potential of radiographic studies and to demonstrate that changes in root morphology can be correlated with crown shape and relative size.

Introduction

A significant proportion of the research effort of palaeoanthropologists is occupied by the study of teeth. Indeed, some critics would claim that palaeoanthropologists are unhealthily preoccupied with the finer points of dental morphology, and their application to obscurantist taxonomic arguments. In the past criticisms such as these would have been hard to refute. For too long teeth were regarded merely as objects for description, and the views of experienced, but inevitably subjective and opinionated, observers were considered adequate judgement. Scant regard was paid to, or allowance made for, ranges of variation of tooth size and expression of morphological features, and little or no attempt was made to quantify and assess the significance of any differences. However, just as other research fields have absorbed and benefited from developments in statistical theory and method, and in particular from newer concepts of population variation and sampling, these same innovations have been incorporated into hominid palaeontological research. The image of the bespectacled professor equipped with calipers and a single fossil pronouncing authoritatively on the pattern of human evolution is long dead, but critics, and to some extent the public, will not willingly let it rest.

In the past decade or so, hominid palaeontology has seen another shift of research emphasis. There has been a move away from merely documenting the past, and a move towards understanding the broader biological context of hominid evolution. In an elegant analysis of the epistemology of hominid palaeontology, Tattersall & Eldredge (1977) have urged that, when hypotheses are made about hominid evolution, more regard should be paid to the level of complexity inherent in each hypothesis. They suggest that three levels should be recognized. At the first level are hypotheses that seek to identify morphological sets, or phena, of hominids and arrange them in a branching diagram based on the distribution of unique features. The second level develops the simpler hypotheses to include propositions about ancestor–descendant relations. The third level hypotheses they call 'scenarios'. These are complex hypotheses that attempt to explain the adaptive and functional reasons underlying evolutionary trends, and the complicated reciprocal relationships between morphology and behaviour. In summary, the two lower levels of hypotheses answer the question, how?; the third level seeks to answer the question, why?

Functional interpretations of teeth

Teeth can make their own special contribution to attempts to devise alternative evolutionary 'scenarios'. Analogues developed from studies of modern primate teeth have made it possible to use the morphology of fossil teeth to make interpretations about diet and social behaviour. In a series of reports, Kay (1975, 1978) developed a system of metrical analysis of molar teeth that differentiates between the shearing and crushing function of the tooth. Leaf-eating species tend to have relatively higher cusps, longer shearing blades and larger crushing basins for a given tooth length than have fruit-eating taxa. These features are presumably adaptations to the diet of leaves, which, because of their toughness and relatively low energy value, require more chewing and processing than fruit. Using these functional correlations, Kay (1977) has examined the diets of Miocene hominoids, but this method has yet to be applied to the study of hominid teeth.

Dietary regimes in extant primates have been correlated with tooth size as well as tooth morphology. When the crown areas of molar teeth are considered in relation to body size, frugivorous species tend to have relatively smaller teeth than do folivores or insectivores (Kay 1973, 1975). However, body size and diet are not independent variables and the relationship between tooth size and diet in primates is a complex one (Pilbeam & Gould 1974; Goldstein *et al.* 1978). The relative size of teeth within a dentition has also been linked with dietary preferences; frugivores are distinguished by their relatively large incisors (Hylander 1975), which they use to dehusk fruits and seeds.

Studies have also sought to relate tooth size with social behaviour. Relative canine size has been examined in relation to social organization, and Harvey *et al.* (1978) found that sexual dimorphism in canine size was greatest in taxa in which intragroup selection and predator pressures are significant influences.

Complementing these studies of the functional correlates of dental morphology are research programmes in which the ways that teeth are worn during life are investigated. In these studies the effects of mastication are usually examined; but examples of non-masticatory tooth use in modern human populations may also be relevant to the study of hominid teeth (Molnar 1972). Most of the literature on tooth wear relates to studies on modern human populations in which attempts have been made to correlate diet with quite gross indicators of dental wear (Molnar 1971). Macroscopic and low power microscopic studies of wear patterns in hominid teeth have also been used to examine hypotheses about dietary specialization of early hominid taxa (Wallace 1973, 1975). Scanning electronmicroscopy now allows the examination of fine details of enamel wear. These studies are still in their early stages, but preliminary results suggest that particular diets are associated with recognizable patterns of enamel microwear (Walker 1979, and this symposium).

The place of systematic studies

Present and future attempts to use hominid dental evidence to interpret dietary preferences and possibly even social organization are likely to make significant contributions towards our knowledge of early hominid behaviour and adaptation. However, the quite proper growth of interest in these research activities has tended to deflect interest away from, and even lead to the denigration of, studies in which teeth are used as guides to morphological groupings and phylogenetic relationships. The result is that the study of dental morphology in the context of hominid systematics is being neglected.

Hominid systematic studies seek to identify and assess patterns of morphological diversity in the hominid fossil sample. It is my contention that functional interpretations and the framing of complex hypotheses about behavioural adaptations can only proceed within a proper systematic framework. Unless workers first put forward hypotheses about the taxonomic significance of the morphological variation within the fossil record, functional interpretations can only be of the most general kind. For instance, unless one attempts to establish how many hominid taxa are represented in the fossil record, how can any differences in behaviour and adaptation of synchronic taxa be usefully discussed? Thus, even in a meeting that quite properly lays stress on attempts to reconstruct hominid behaviour, and reactionary though it may seem, I propose to examine some of the ways in which dental evidence can contribute to hominid systematic studies.

Have teeth a special contribution to make?

It is important that systematic studies proceed in a logical sequence (Simpson 1963; Wood 1978). The initial steps are the identification of patterns of morphology in the fossil sample and the recognition, and attempted definition of, morphological groups or 'phena'. These studies are then followed by attempts to assess the taxonomic significance of the morphological groupings and to establish any probable phylogenetic relationships among the phena. Teeth are so crucial to the survival of individuals and play such an important part in the adaptation of breeding groups to their environment that their importance in evolutionary studies is seldom questioned. However, two further properties of teeth give them additional importance. The first is a consequence of the development and structure of dental enamel, and the second relates to the contribution teeth make to the fossil record.

Although bone and tooth enamel are both mineralized tissues with a crystallite component, they differ both in their ontogenetic development and in their capacity to modify their form after maturation. Teeth develop in such a way that, after the enamel cap of the tooth crown has developed in the dental follicle, the capacity to modify crown morphology is lost. Enamel is made up of regularly orientated crystallites, which form prisms, the basic units of its structure. Enamel formation or amelogenesis starts at the boundary with the dentine and proceeds towards the eventual outer surface of the tooth crown. Before the eruption of the tooth the enamel-forming epithelial layer ceases to become active and is finally shed. Once amelogenesis has ceased, crown morphology can only be altered by the exigencies of attrition, abrasion and erosion. Thus enamel shape and size represent a faithful record of the combination of genetic and environmental influences that control and affect amelogenesis.

Bone, in contrast to enamel, does not lose its capacity to modify its size and shape. Although growth in length of long bones ceases when the cartilage forming epiphysial plates degenerates, the capacity for circumferential growth and remodelling is retained by virtue of the osteogenic potential of the periosteum. Experiments have demonstrated the capacity of bone to modify its form in response to changes in the pattern of external stresses (Washburn 1947*a*, *b*; Riesenfeld 1969, 1972, 1974; Burstein *et al.* 1972). Just how much of the morphology of a bone is a reflection of the loading conditions to which it was subjected during life is unknown; indeed there is debate about whether sustained submaximal stress, or infrequent, but high, loadings are the more important determinants. Thus, whereas the phenotypic plasticity of bone contributes an additional potential variable when morphological variation is being assessed, this additional factor can be discounted when assessing the significance of differences in tooth crown size and shape.

A second reason to pay special attention to patterns of dental variation is the fact that teeth are particularly well represented in the fossil record. The different rates of survival of skeletal parts during fossilization are determined by many factors. In some conditions, for example, when the skeleton is weathering by exposure to extremes of temperature and moisture, teeth tend to crack and disintegrate; this is probably related to the low tensile strength and brittleness of the enamel. However, in most phases of the process of fossilization the hardness of the inorganic materials that go to make up the structure of teeth ensure their differential survival. Enamel, which covers the tooth crown, is 96 % (by mass) mineral. It is the hardest tissue in the body, and the important surface regions are harder than the deeper layers. Enamel has a high modulus of elasticity and is particularly rigid. These characteristics, together with the compact shape of hominid tooth crowns, contribute to the particular durability of teeth in most of the depositional environments in which hominid fossils are preserved. A census of the skeletal parts found at fourteen hominid sites (Tobias 1972) showed that, at the five South African and nine east African sites examined, teeth made up respectively 75 % and 70 % of the total sample. However, by pooling the east African data, major disparities in the contribution that teeth make to the body of hominid fossil evidence at individual sites are masked. Omo and Koobi Fora are both fossil sites in the Lake Turkana Basin. However, the depositional environments at the Omo are mainly associated with the flood plain of a large perennial river system, whereas at Koobi Fora the fossils were deposited in lake margin and small ephemeral channel environments (de Heinzelin *et al.* 1976; Findlater 1978). In a study in which the proportions of skeletal parts preserved in fluvial and lake margin environments at Koobi Fora were compared, Behrensmeyer (1975, 1978) demonstrated that in fluvial deposits denser skeletal components, such as teeth, survived better. This effect of hydraulic sorting before sedimentation is evident when the hominid samples at Omo and Koobi Fora are compared. If each well preserved tooth is taken as an individual specimen, teeth make up nearly 90% of the hominid sample at the Omo, whereas they constitute less than 60% at Koobi Fora; if the proportions of specimens that are isolated teeth are compared, the disparity is even more marked. Thus, though at all sites dental remains are a major component of the hominid fossil sample, at some sites, such as Omo in Ethiopia and Laetoli in Tanzania, any deductions about the hominids represented in these samples are based almost entirely on dental evidence.

WHAT EVIDENCE DO TEETH PROVIDE?

The crown and roots of teeth potentially provide a formidable amount of morphological and metrical data. Nonetheless, discussions of the pattern and significance of variation in early hominid dental remains are often limited to relatively crude length and breadth measurements of tooth crowns (see, for example, Wolpoff 1971). In the remainder of this paper the types of dental evidence that are available are reviewed and methods for their analysis are discussed. Most of the examples cited are from comparative studies of teeth associated with 'robust' australopithecines. The theme of the review is a question: can 'robust' australopithecine teeth and dentitions be distinguished from those of other taxa? The review is not intended to be an exhaustive survey of the literature, and its emphasis on relative tooth size and the detailed analysis of canine and molar teeth reflects my particular research interests.

Crown size

The usual way to quantify the size of a tooth crown is to measure its maximum length and width, and to use either these measurements on their own, or their product, for comparative studies. Since, on the basis of such measurements, differences in length of 2 mm or less have been considered taxonomically significant (Tobias 1966), it would be prudent to examine briefly factors that affect the accuracy, reliability and descriptive utility of this type of data.

The accuracy and reproducibility of measurements are affected by both the shape of the crown and the degree of wear on the tooth. The definition of terminus points for simple crown measurements is particularly difficult for those teeth, such as upper molars, that have an irregular crown outline. Mesiodistal length of upper molars can be taken either as the 'maximum' length (Korenhof 1960) or the distance between the points of contact with neighbouring teeth. In our experience there are sometimes significant differences between these measurements on the same tooth; this point has also been noted by Tobias (1967). It is equally difficult to define terminus points for taking buccolingual breadth that give consistent results; these difficulties are increased when isolated teeth are measured. In a survey of the dental remains from Koobi Fora, repeated buccolingual measurements in the same upper molar by two experienced observers, using the same protocol, in some cases resulted in discrepancies of between 0.5 and 1 mm.

While patterns of tooth wear provide information about dental function and perhaps also taxonomic affinity (Wallace 1975), wear adversely affects the reliability of dental measurements. A particular problem is the influence of approximal wear on mediodistal crown lengths. Ideally two values should be cited, the 'actual' mesiodistal length and the 'estimated' unworn length. This estimation can be made by a combination of extrapolating the unworn parts of the occlusal surface contour and, if dentine is exposed, making an estimate of enamel thickness; corrections of about 5 % of the 'actual' mediodistal length are quite common for worn molar teeth.

The value, for comparative purposes, of crown area, when computed from simple length and breadth measurements, depends very much on the shape of the occlusal outline of the tooth. As part of a comprehensive metrical and morphological survey of Plio-Pleistocene hominid dental remains, we have prepared magnified photographs of the occlusal view of each tooth. The basal outline of the crown was defined, and the area of the crown determined by planimetry. Crown area measured directly in this way was compared to the crown area derived from the product of the buccolingual and 'estimated' mediodistal diameters by expressing it as a percentage of the derived crown area value. In mandibular first molars the crown area by planimetry was, on average, 83 % of the derived area, with a range between 74 % and 93 %; in second and third molars the range was even greater. Thus crown area computed from length and breadth measurements is a relatively unreliable estimate of the actual area of a tooth, and this point should be borne in mind when the significance of differences in derived crown area estimates in fossil samples are assessed.

One of the current problems of hominid systematics is the significance of the dental differences between the 'gracile' and 'robust' australopithecines. The hypodigm of the gracile australopithecines is usually taken to include material recovered from Member 4 at Sterkfontein and the deposits at Makapansgat and Taung; it has recently been much expanded by the addition of newly discovered specimens from Sterkfontein (Tobias 1978), but as yet no detailed data on this new material are available. The robust australopithecine sample includes the hypodigms of two taxa, *Australopithecus* (*Paranthropus*) *robustus* from South Africa, and *Australopithecus* (*Paranthropus*) *boisei* from East African sites. The derived crown areas of the canines and molars shown in figure 1 are based on data from the standard odontography of this material (Robinson 1956) and on measurements taken by the author. The ranges of canine base area and molar crown area of *Australopithecus africanus* and *Australopithecus* (*Paranthropus*) *robustus* overlap, and if these data are pooled a unimodal distribution results. Although teeth with crown areas in the non-overlapping parts of the ranges could be reliably assigned to one taxon or the other, the distribution of the values is such that many specimens could not be accurately assigned on the basis of size alone. The sample of *Australopithecus* (*Paranthropus*) *boisei* is small because it only includes teeth in mandibles or crania that have been taxonomically assigned on the basis of features other than dental ones. In molar size there is little or no overlap between *Australopithecus africanus* and *Australopithecus* (*Paranthropus*) *boisei*; similarly impressive differences in crown area are seen between teeth from the lower members of the Shungura Formation, and those in members E through to G, which have been attributed to, or closely compared with, *Australopithecus* (*Paranthropus*) *boisei*.

In addition to the sizes of individual teeth, the relative sizes of teeth within each taxa or even in individual dentitions can also be compared. Robinson (1956) pointed out that gracile and robust australopithecines from the South African sites could be distinguished on the basis of relative canine size, which is usually expressed by relating canine base area to molar crown area. While there is general acceptance that robust australopithecines do have relatively small canines, the significance of these differences is still debated. Robinson (1956) claims that differences in relative canine size indicate dietary specialization in the 'robust' taxon, whereas Brace (1967, 1972), Pilbeam & Gould (1974) and Wolpoff (1978) consider that differences in

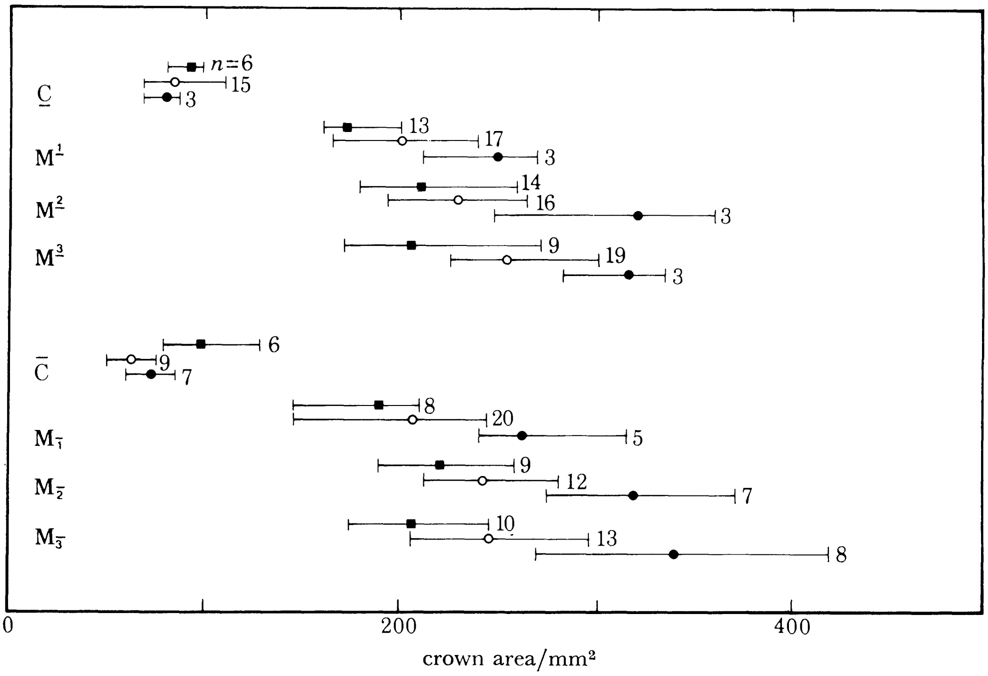

Figure 1. Crown base areas of canines and crown areas of molars, computed from measurements of length and breadth. Means, sample range and number of specimens (n) used are indicated for each taxon. Measurements for *Australopithecus africanus* (■) and *Australopithecus* (*Paranthropus*) *robustus* (○) are taken from Robinson (1956). The sample of *Australopithecus* (*Paranthropus*) *boisei* (●) comprises: Chesowanja, CHI; Peninj; OH5; KNM-ER 729, 3230; and Omo 7A-125, 74-21, F 22-1a and b.

dental proportions are simply due to the scaling effects of the larger body size of the robust form, which has been estimated to be between 10 to 25% greater than that of the gracile australopithecines. To test whether the differences in relative canine size are merely the response of allometric growth to an increase in body size, we must seek the most appropriate model for tooth–body size relations in hominid taxa. There are logical objections to generating a model from the fossil groups themselves. Allometric trends determined in this way necessarily reflect the choice of sample, and workers who then use the presence of such trends to discount any significant differences within the fossil sample are engaged in a circular argument. As an alternative tooth–body size relations in five modern primate taxa have been examined (Stack & Wood 1980). Three models of tooth–body size relations were studied: sexes of each taxon examined separately; the combined sex sample for each taxon; and the interspecific relationship between the four non-human taxa (Wood 1979). In all three models the rate of increase in canine size exceeded, or was not significantly different to, the rate of increase in molar size. Thus if gracile australopithecines, or creatures closely resembling them, are ancestral to the robust taxa (Tobias 1978; Johanson & White 1979), then there has been selection, apparently against allometric trends, for canine reduction in the larger-bodied robust australopithecines. The implication is that these differences have more taxonomic significance than if they were simply scale phenomena.

Crown shape

Relatively few comparative studies have made detailed reference to tooth crown morphology (Robinson 1956; Korenhof 1960; Frisch 1965; Tobias 1967; Sperber 1974). In those studies in which close attention has been paid to patterns of variation in mandibular molar morphology, the relative size of the cusps, the incidence of extra cusps and the presence of cingulum remnants (and the pattern of the main intercuspal fissures) have been the most commonly used distinguishing features. In a review of the differences between the gracile and robust australopithecines, Robinson (1956) acknowledges that 'morphologically the mandibular molars of *Paranthropus* and *Australopithecus* are manifestly very similar'. Nonetheless, he draws attention to several morphological features whose expression differs in the two samples; these include the presence of a protostylid and its effect on the shape of the buccal face in *Australopithecus*, the presence on $M_{\bar{1}}$ of an additional distal cusp, or C6, in *Paranthropus*, and the tendency for *Australopithecus* to have a $+$-shaped fissure pattern.

We were interested to try to quantify the type of differences noted by Robinson. Detailed occlusal view photographs and plaster casts were made of all available premolar and molar tooth crowns. In teeth where the course of the fissures could still be traced, the boundaries of the main cusps, any additional sixth or seventh cusps and the outline of the protostylid were defined on the photographs, and the areas of all these elements were measured by planimetry. Sperber (1974) has previously examined the cusp areas of the South African hominid molars, but he used area values derived from length and breadth measurements of each cusp. Individual cusp area data have been analysed by principal components analysis. Preliminary data on cusp areas, expressed relative to the overall size of the first mandibular molar, show that the first principal component discriminates between teeth attributed to the gracile and robust australopithecines; the cusp areas that contribute most to this separation are the protoconid and entoconid.

The results of our observations on the incidence of an accessory sixth cusp concur with those of Robinson; distal cusps are a regular feature of robust australopithecine mandibular first molars, but according to our classification no gracile australopithecine first mandibular molar has conclusive evidence of such a cusp. In modern human populations accessory cusp formation has been associated with tooth size (Dahlberg 1961; Garn *et al.* 1966). Preliminary analysis of data suggests a similar association in fossil hominid teeth, but the factors that determine whether the extra cusp should be distal or lingual are as yet unknown. Robinson's claim that the protostylid cingulum remnant is more common in gracile than robust australopithecine molars is not supported by our investigation.

In previous studies attempts have been made to analyse fissure pattern from the coordinates of defined points on the fissure system (Biggerstaff 1969, 1975; Lavelle 1978). Detailed linear, not coordinate, measurements of mandibular molar crowns have been taken on a series of living and fossil hominoids (Corruccini 1977), but this method has so far not been used to test for patterns of variability within the hominid sample. We have defined a maximum set of 26 reference points on the mandibular molar fissure pattern, each point is located by its x and y coordinates. The definitions of the reference points are such that the same system can be used to examine the teeth of Miocene hominoids and non-human primates. Analysis of these data, and also the analysis of the shapes of crown profiles, are still in progress, and the results will be reported in due course.

Subocclusal morphology

The shape and size of tooth roots are seldom referred to in surveys of early hominid dental morphology. While it is true that few isolated teeth are found with both roots and crowns

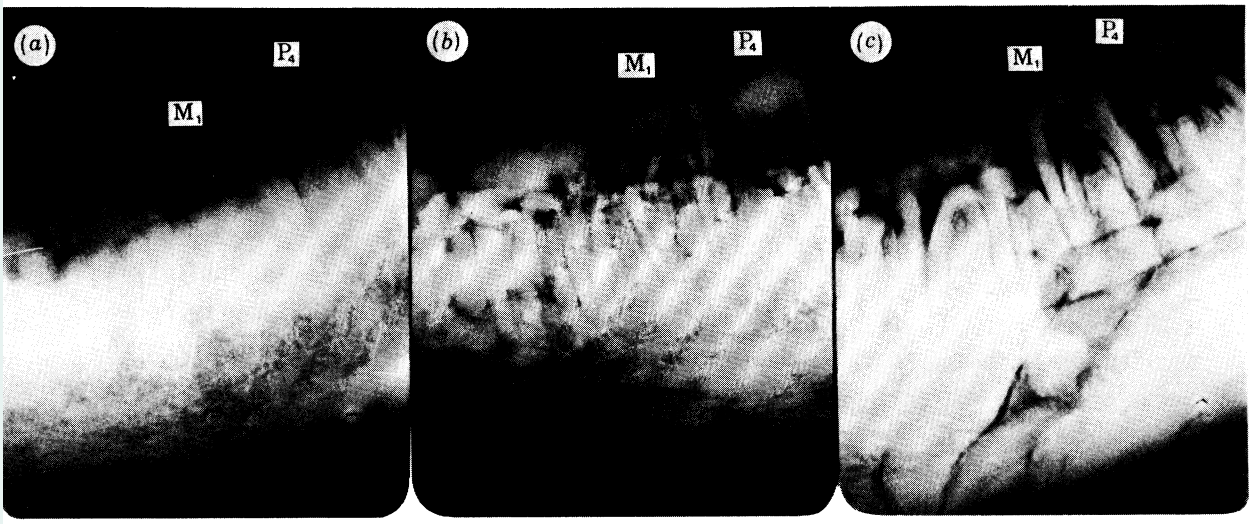

Figure 2. Lateral radiographs of mandibles attributed to *Australopithecus* (*Paranthropus*) *boisei*: (*a*) Peninj; (*b*) KNM-ER 3230; (*c*) KNM-ER 729. Thick lines on the grid are separated by 5 mm. Radiographs taken by Susan Abbott.

intact, information about root number can often be obtained by careful observation of the damaged alveolar borders of upper and lower jaws. Radiography also provides a means of examining roots that lie within mandibles or maxillae. Robinson (1956) and Sperber (1974) have paid particular attention to root form, and Sperber's study was the first major radiographic survey of early hominid material.

As a contribution to the analysis of the cranial remains from Koobi Fora we have undertaken a radiographic survey of the dental, mandibular and maxillary specimens from Koobi Fora, Olduvai, Peninj and Laetoli. One of the interesting findings is the range of morphology in the roots of the lower premolars. Robinson (1956) and Sperber (1974) both reported that all lower premolars in which the roots could be discerned were double-rooted, with the exception of one $P_{\bar{4}}$, which has three roots. A feature of the lower premolar crowns in the robust australopithecines is the excessive development of the talonid, with accessory cusp formation on the distal marginal ridge and a large posterior fovea (Robinson 1956; Howell 1978). This molarization' of the posterior premolar results in the $P_{\bar{4}}$ dimensions significantly exceeding those of $P_{\bar{3}}$. Radiographic images of the roots of $P_{\bar{4}}$ in KNM-ER 729, KNM-ER 3230 and the Peninj mandible are similar in shape and length to those of the molar teeth; indeed in some cases $P_{\bar{4}}$ roots are larger than those of $M_{\bar{1}}$. (figure 2). Careful assessments of comparative root lengths and inclinations, and investigations of the relationship between root size and morphology and crown size and shape have yet to be made. Nonetheless, our preliminary observations encourage us to believe that details of subocclusal morphology will make a useful contribution to the analysis of patterns of variation of early hominid tooth morphology.

Conclusions

A distinction has to be made between the ability to demonstrate differences between taxa by means of sample parameters and that to assign individual specimens to a taxon. It is clear from this review and other studies that there is sufficient overlap between the gracile and robust australopithecines in simple tooth dimensions for tooth size alone to be ineffective as an indicator of taxonomic affinity. The continuously distributed nature of morphological features, the difficulties of defining them and the generally small sample sizes also reduce the efficacy of morphological traits as taxonomic discriminators.

This review has highlighted the need for more vigorous attempts to standardize and quantify information about tooth size and shape. Simple length and breadth measurements are clearly inadequate to describe and compare a structure as complicated as a tooth. Preliminary results of an odontometric analysis of early hominid molar and premolar morphology suggest that a multivariate approach may help to establish a more rigorous definition and description of the dental characteristics of a taxon. Data such as these would provide a framework on which to test hypotheses of morphological diversity, and may also allow a more objective assessment of the affinities of individual specimens.

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LORD ZUCKERMAN, F.R.S. (*The Zoological Society of London, Regent's Park, London NW1 4RY, U.K.*). Dr Wood has told us that (to quote his own words) 'in establishing phylogenetic relationships in a systematic framework' he defines his morphological groups before assessing the significance of the differences between them. This sounds quite logical. But would he now tell us what assumptions underlie the first stage of the process?

B. A. WOOD. I had tried to make the point early in my talk that establishment of phylogenetic relationships should be the last of a number of stages in any attempted analysis of hominid fossil evidence. The first stage is to break the fossil sample into a series of subgroups based on morphological features and morphometric criteria. The criteria for these subgroups is not that there are no differences between the fossils in each group, i.e., no variation, but that the variation is more likely to be intraspecific rather than interspecific. Because we have no *a priori* knowledge of the patterns of variation in fossil taxa, I claim that we have to rely on 'models' of variation derived from appropriate modern taxa.

The second and third stages of any analysis are to establish the systematic relationships of the morphological subgroups. For example, are they conspecific or congeneric? To do this again means making subjective judgements of patterns of variation, again based on analogies drawn from extant taxa. The last stage, phylogenetic analysis, requires that we establish a series of morphoclines by trying to trace the transmission and modification of morphological features.

At all levels the analytical process is weak because it involves argument by analogy, but surely this is preferable to the circularity of making assumptions about what specimens make up fossil taxa. I stressed in my talk the importance of the results of the principal components analysis of the tooth crown data because this type of analysis makes no *a priori* assumptions about groups; as Lord Zuckerman knows it seeks major axes of variation, and in this case the major axis of variation sorts mandibular molar tooth crown morphology into groups that happen to be in agreement with the conventional taxonomic attribution of this material.

I have no defence against any accusation that decisions about classification are subjective; my aim has been to reduce the subjectivity to the lowest possible level.

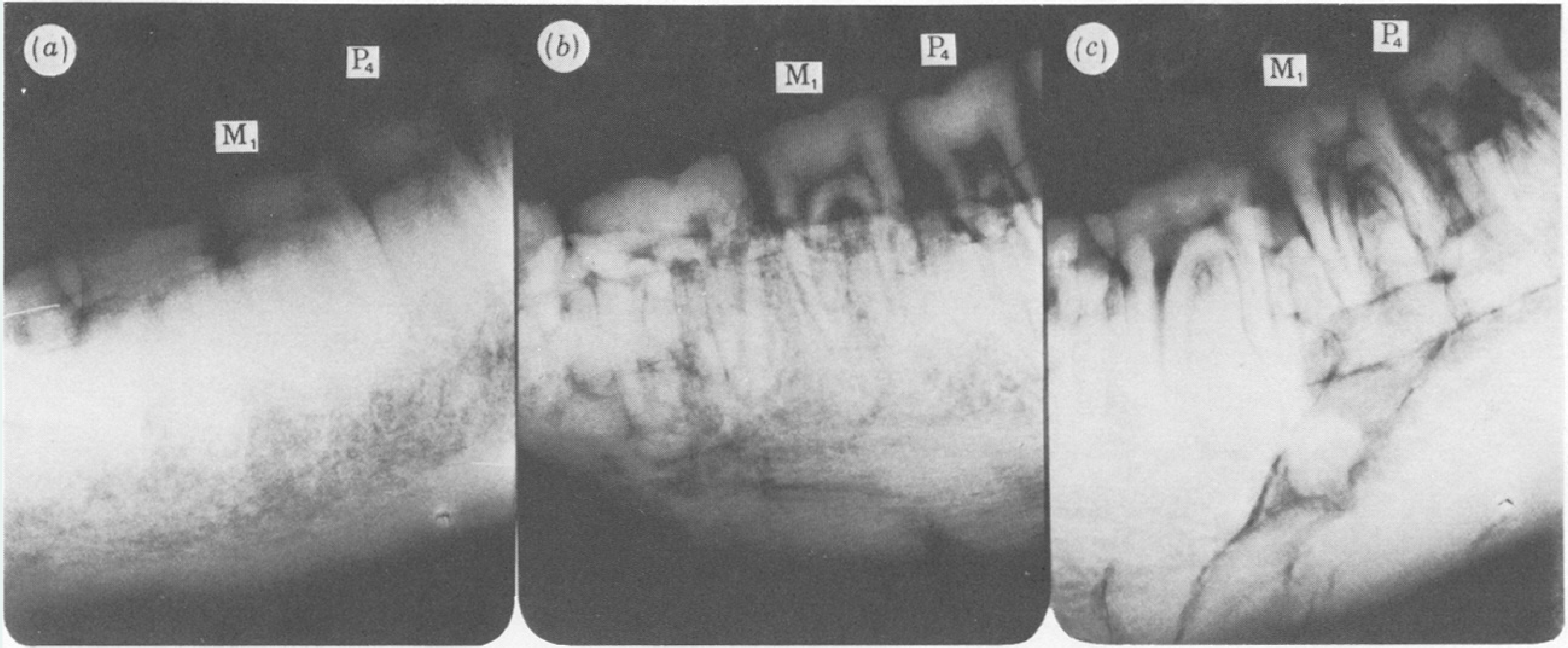

FIGURE 2. Lateral radiographs of mandibles attributed to *Australopithecus* (*Paranthropus*) *boisei*: (*a*) Peninj; (*b*) KNM-ER 3230; (*c*) KNM-ER 729. Thick lines on the grid are separated by 5 mm. Radiographs taken by Susan Abbott.