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Australopithecine Enamel Prism Patterns

Abstract. *Following a recent suggestion that tooth enamel prism shape differs within Hominoidea, the teeth of a number of extinct and extant hominoid species were analyzed by scanning electron microscopy. The enamel prism patterns of some gracile and robust australopithecine specimens from Sterkfontein, Swartkrans, and Kromdraai are recorded. The characteristic arrangements of enamel prisms in all modern and extinct hominoid species were found to be essentially similar. The implications of enamel prisms for phylogenetic deduction in Hominoidea are discussed.*

Recent electron microscopic work has shown that the division of tooth enamel into prisms is primarily due to the repetitive orientation of the minute crystallites which compose the inorganic part of the enamel. Analysis of the different patterns assumed by the enamel prisms in various mammalian dentitions has led several workers to conclude that enamel structure permits designation to particular taxonomic groups (*1*). Boyde (*2–4*) has summarized and added much to the state of knowledge of the distribution of prism patterns in mammals (Fig. 1). A recent scanning electron microscopic study of the teeth of selected hominoid primates has suggested that the extant pongids have a prism pattern distinctly different from that of *Homo sapiens* (*5*). Gantt *et al.* (*5*) applied this technique of prism analysis to the Miocene hominoid *Ramapithecus* in an attempt to shed light on the controversial phylogenetic status of this primate (*6*). They recorded a prism pattern for *Ramapithecus* (*5*) which is similar to that of *H. sapiens* (Fig. 1c) and unlike the circular or hexagonal patterns which they described for the pongids (Fig. 1a). It was noted that prism patterns may be of potential use for functional analyses as well as phylogenetic and taxonomic purposes (*5*).

The purpose of the study reported here is to record the enamel prism patterns found in several australopithecine specimens from the Transvaal limestone caves, to compare them with those found in other hominoids, and to discuss the potential of prism patterns for phylogenetic deduction in the Hominoidea.

The gracile australopithecine sample which was examined included STS 21 (RM^2), STS 4 (LM_2), STS 49 (LP^3), and STS 1881 (LM^3) from Sterkfontein Member 4. The sample of robust australopithecine teeth comprised SK 855 (LM_3), SK 74c (RP^4), SK 875 (fragment), and SK 879 (fragment) from Swartkrans Member 1 and TM 1603 (LM^3), TM 1517 (LM^2), two recently excavated teeth KB 5223 (LM_1), and a heavily worn molar fragment (KB 5222) from the Kromdraai australopithecine site (*7*, *8*). The extant comparative series included a number of permanent premolars and molars of *Pan troglodytes* ($N = 2$ individuals), *Gorilla gorilla* ($N = 1$), *Pongo pygmaeus* ($N = 3$), and *H. sapiens* ($N = 4$). The specimens were prepared for examination in the microscope as outlined previously (*5*), and examined in a JEOL JSM-35 scanning electron microscope at various magnifications. On each specimen all available surfaces (occlusal, buccal, lingual, mesial, and distal) were studied. In each case the tooth was rotated so that the heads of prisms were perpendicular or nearly perpendicular to the electron beam.

On all hominid and pongid specimens pattern 3 (Fig. 1c), also referred to as the keyhole pattern, was found to predominate on all surfaces examined (Figs. 2a, 3a, and 4a). Other prism configurations (Figs. 2, b and c, 3b, and 4b) were encountered on the teeth of each species, but these occurred in isolated patches only. In both hominids and pongids of the present sample pattern 1 (Fig. 1a) was restricted to the occlusal surfaces, and apparently associated with cuspal convexities (Figs. 2b and 3b). Prism configurations which approached those of pattern 2 (Fig. 1b) were present in patches on teeth of each species,

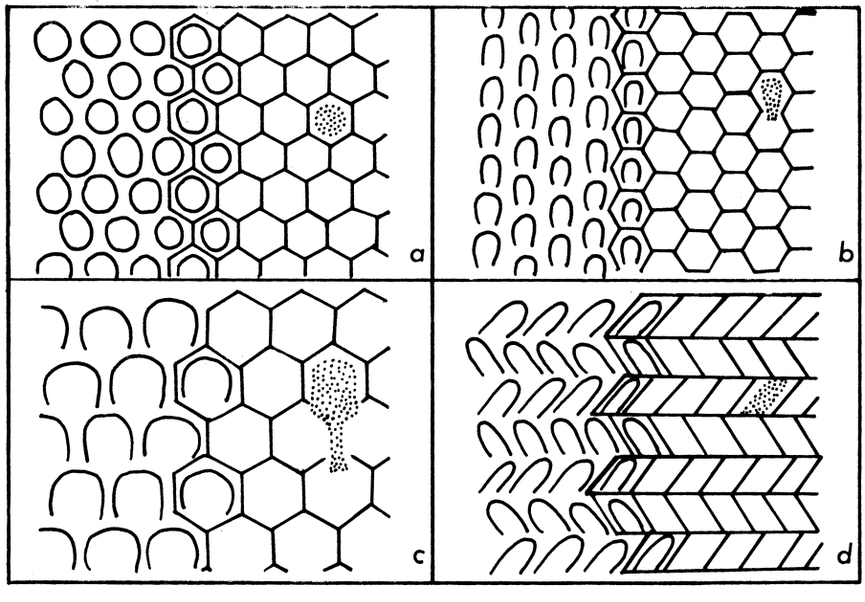

Fig. 1. Schematic representation of prism patterns in the enamel of mammals. Each diagram shows on the left the prism boundaries or sheaths, which represent planes of abrupt change in crystallite orientation within the enamel; on the right the secretory territories of the ameloblasts; and in the middle the relationship of prism sheaths to the secretory territories. The stippling represents the areas which are defined as prisms in the various patterns. (a) Pattern 1, predominant in members of the orders Cetacea (Odontoceti), Insectivora, Chiroptera, and Sirenia. (b) Pattern 2, in Ungulata and Marsupialia, also in primates. (c) Pattern 3, in Primates, Carnivora, and Proboscidea. (d) Pattern R (modified pattern 2), in rodent incisors. Only in pattern 3 enamel (c) is all the enamel attributable to prisms; although they are of exactly the same composition, we refer to interprismatic regions in the other prism patterns. [Adapted from figure 1 in (*2*) and figures 5 to 8 in (*4*)]

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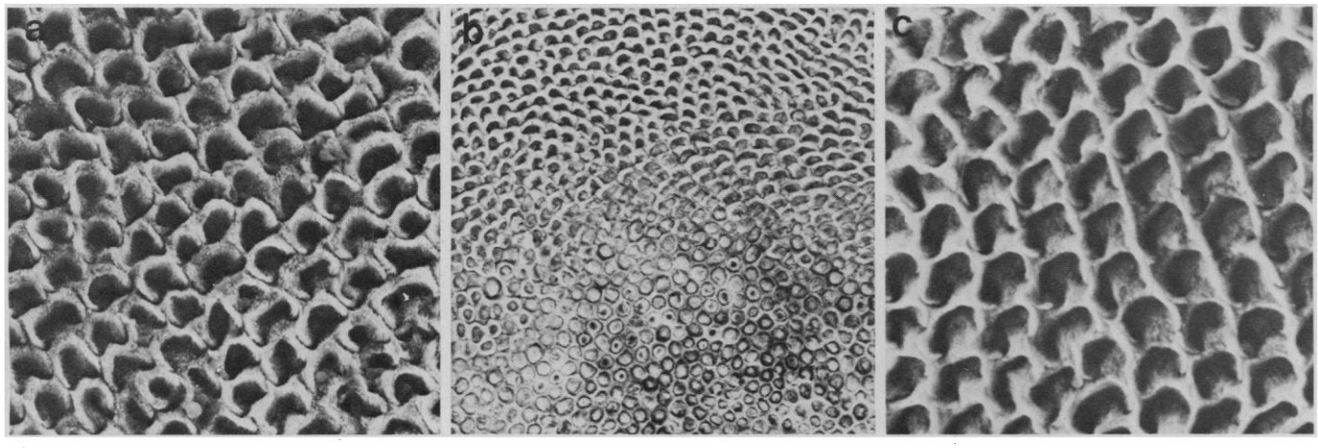

Fig. 2. Scanning electron micrographs of enamel prism patterns in *Australopithecus africanus*: (a) STS 4, ×1500; (b) STS 21, ×500; and (c) STS 21, ×1500.

sometimes on occlusal and sometimes on nonocclusal surfaces (Figs. 2c, 3b, and 4b). The latter arrangement appeared to be more common on chimpanzee teeth than on those of other pongid species. The incidence of prism configurations approaching pattern 2 was also more prevalent on the gracile than on the robust australopithecine specimens. Furthermore, Figs. 2 to 4 clearly show the effects of differential acid etching, which have been discussed with respect to prism patterns in human teeth (*9*). In some instances the "heads" or centers of the prisms were removed (Figs. 2, a and c, and 4b), while in others the "sheaths" or prism junctions were preferentially demineralized (Figs. 3, a and b, and 4a).

Boyde (*4*) has suggested that there is a "correlation between the size and shape of prisms" which is "not merely confined to species differences." More specifically, he (*4*) has shown that the prisms of pattern 3, irrespective of the taxon in which they are found, are considerably larger than those of pattern 1, and that pattern 2 and pattern R prisms (Fig. 1) tend to be the smallest. It is known that prism sizes vary on any one tooth in response to such factors as relative proximity to dentinal and coronal surfaces, differential prism crowding due to tooth surface topography, and abnormal enamel development. In terms of a correlation between prism size and shape, predominant prism patterns may be expected to be interspersed with alternative patterns in areas of atypical prism sizes. In fact, this does occur in *H. sapiens* (*10*) and other mammalian species (*4*), and in all the hominoid species included in the present study. Measurements of prisms in the present sample corroborate the suggestion of Boyde (*4*) that prisms of pattern 3 are larger than those of pattern 1, whether measured on the same individual tooth (Figs. 2b and 3b) or on teeth of different hominoid species.

In conclusion, the results of this investigation indicate that in both the Hominidae (australopithecines and recent *Homo*) and extant Pongidae the characteristic arrangement of enamel prisms conforms to the keyhole or pattern 3 configuration. The results suggest that gross prism morphology contains no information on phylogenetic relationships of hominoid species. Even if detailed

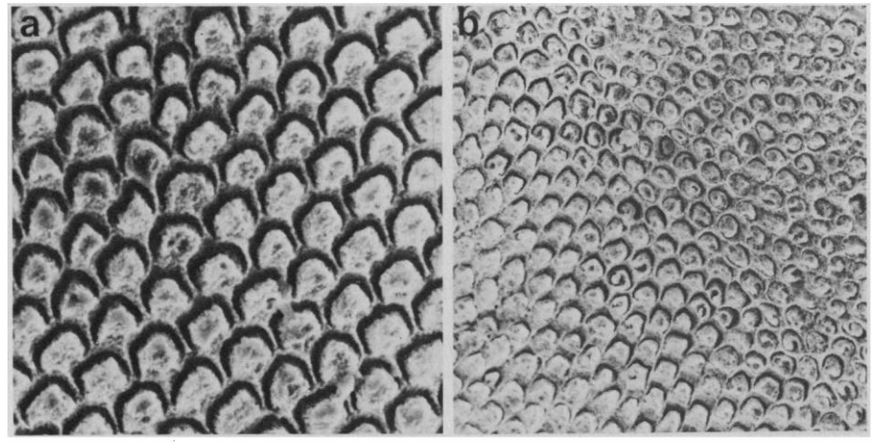

Fig. 3. Scanning electron micrographs of enamel prism patterns in *Australopithecus robustus*: (a) SK 879, ×1500; and (b) TM 1603, ×500.

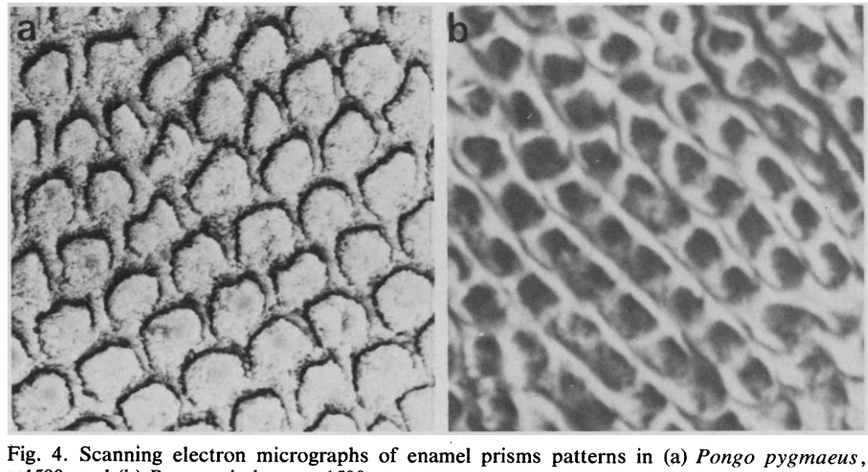

Fig. 4. Scanning electron micrographs of enamel prisms patterns in (a) *Pongo pygmaeus*, ×1500; and (b) *Pan troglodytes*, ×1500.

studies were to demonstrate proportional differences between pongid and hominid species in the incidence of minor configurations (patterns 1 and 2), only the component of such differences that is independent of size (if any such component exists) would be useful in phylogenetic deduction. The occurrence by itself of a prismatic keyhole pattern in *Ramapithecus* suggests no closer kinship of that taxon to *H. sapiens* than to the extant apes.

ELISABETH S. VRBA
Transvaal Museum, Post Office Box 413, Pretoria, 0001 South Africa
FRED E. GRINE
Medical School, Department of Anatomy, University of the Witwatersrand, Johannesburg, 2001 South Africa

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7. For stratigraphic details on Sterkfontein, see T. C. Partridge [*Nature (London)*, in press]; on Swartkrans, C. K. Brain [*S. Afr. J. Sci.* **72**, 141 (1976)]; and on Kromdraai, C. K. Brain [*Transvaal Mus. Mem.* **13**, 1 (1958)]. New specimens excavated at Kromdraai during 1978 will be announced shortly by E.S.V.
8. Abbreviations used in identifying teeth: R, right; M, molar; L, left; and P, premolar. Numerical subscripts and superscripts give the position of the tooth and whether it is an upper (superscript) or lower (subscript) one. Thus, RM^2 is the second right upper molar.
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11. We thank C. Frick of the Geological Survey of South Africa and M. J. Whitcomb of the University of the Witwatersrand for allowing us access to scanning electron microscopes, and S. C. Kammeyer and D. C. Panagos for technical assistance. Discussions with and comments from L. M. Jonck, P. Cleaton-Jones, P. V. Tobias, and C. K. Brain are gratefully acknowledged.

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Rapid Changes in Brain Benzodiazepine Receptors After Experimental Seizures

Abstract. *Seizures induced in the rat by electroshock or by injections of pentylenetetrazol increase the specific binding of diazepam to putative receptor sites in cerebral cortical membranes. The enhancement of diazepam binding results from a rapid increase in the number of available binding sites rather than a change in receptor affinity. The postictal increase in cortical benzodiazepine receptors suggests that the cerebral cortex might be more sensitive to the anticonvulsant effects of the benzodiazepines after seizures. This observation may be related to the mechanism of action of these drugs in the treatment of recurrent seizures such as status epilepticus.*

Diazepam and other closely related benzodiazepines are potent anticonvulsants in a wide variety of experimental and clinical seizure disorders; they are especially effective in the treatment of recurrent multiple seizures such as status epilepticus (*1*). Despite the unequivocal efficacy of the benzodiazepines in elevating seizure threshold (*2*) and rapidly inhibiting the spread of epileptic discharges from neocortical and rhinencephalic foci (*1, 3*), little is known about their underlying mechanism of action. Recent reports have demonstrated the presence of saturable, stereospecific, high-affinity diazepam-binding sites in the central nervous system of both rat and man (*4, 5*). Competition for this binding site by other benzodiazepines closely parallels their potency as anticonvulsants (*4, 5*) suggesting that these sites may function as receptors mediating the pharmacological actions of these drugs. If benzodiazepine receptors or their presumed endogenous ligands are related to the anticonvulsant actions of these compounds (*4*), they may normally be involved in the regulation or pathogenesis of seizure activity. We now report that both electrically and chemically induced seizures result in a rapid increase in the number of cortical benzodiazepine receptors without altering the apparent affinity of diazepam for these receptor sites.

Adult (125 to 150 g) male Sprague-Dawley rats (Taconic Farms) housed under standard laboratory conditions, were used in all experiments. Maximum electroshock seizures were induced with a Medicraft electroconvulsive therapy unit (150 V, 1 second, a-c) through ear clips attached to the pinnae (*6*). Generalized seizures, characterized by tonic-clonic movements, lasted for less than 1 minute. Subconvulsive electroshock (70 V, 0.4 second, a-c) was administered in the same manner. Control rats were subjected to the same procedures except that current was not applied. Chemically induced seizures were elicited by a single intraperitoneal injection of pentylenetetrazol (K & K Laboratories) (45 mg/kg in 0.9 percent saline). Control animals received saline alone. Only animals displaying generalized tonic-clonic movements within 2 to 3 minutes of injection were studied. Pentylenetetrazol-treated animals occasionally had free-running or multiple generalized seizures, or both. In order to control for the effects of interictal or postictal hypoxia on diazepam binding, additional rats were rendered hypoxic with argon gas (*7*). No seizures were observed in this group. Rats were killed by decapitation and crude synaptosomal (the second pellet) fractions of cerebral cortex (pooled frontal, temporal, and occipital cortices) were prepared as described (*5*). The final pellet was resuspended in 40 to 50 volumes of cold tris buffer (Calbiochem) (0.05*M*, *p*H 7.4) to a final protein concentration of approximately 1 mg/ml. Total, specific, and nonspecific diazepam binding was measured as described (*5*) with minor modifications (*8*). Specific binding refers to the total binding of [^{3}H]diazepam minus nonspecific binding which was obtained in the presence of 3 μM diazepam. Nonspecific binding was generally less than 5 percent of total binding at concentrations near the apparent dissociation constant (K_d) for diazepam. Nonspecific binding was not significantly affected by any of the experimental conditions, nor did pentylenetetrazol have any effect on diazepam binding in vitro at concentrations up to 1 μM (unpublished observations).

The amount of [^{3}H]diazepam specifically bound to cerebral cortical membranes (crude synaptosomal fraction) increased after seizures had been induced in the rats by electroshock; the binding increased by 21.2 percent ($P < .005$) and 21.4 percent ($P < .001$) at 15 and 30 minutes, respectively (Fig. 1). The binding of [^{3}H]diazepam returned to preseizure levels by 60 minutes. To determine if the changes in cortical diazepam binding were secondary to seizure-induced hypoxia, we investigated the effect of hypoxia on cortical benzodiazepine recep-

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