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# VARIATION IN MOLAR ENAMEL THICKNESS OF THE GENERA *CERCOPITHECUS* AND *COLOBUS*

*ABSTRACT: In the present study, 55 maxillary second molars of six different* Colobus- *and* Cercopithecus-*species* (C. polykomos, P. badius, P. verus, C. campbelli, C. petaurista, C. diana) *were sectioned bucco-lingually through the mesial cusps. Several measures and indices were recorded in order to determine differences in enamel thickness between the species. As has often been postulated without ever having been proven on a sample of considerable size, it has been expected for the predominantly leaf-eating Colobinae to have thinner enamel than the mostly fruit-eating Cercopithecinae. This hypothesis could be confirmed, but only for relative thickness referring to tooth size. Absolutely, most Colobines had generally thicker enamel because of their larger body- and tooth-size, but not* P. verus. *The relatively thin enamel was related to high cusps and could therefore be interpreted as an adaptation to a folivorous diet. Additionally, the enamel was differently distributed over the crown, for in cercopithecine molars, the enamel was substantially thicker on the lingual than on the buccal side, whereas in colobine teeth, the enamel was more equally distributed. This was interpreted as allowing the cusps to be more uniformally abraded resulting in shearing blades that lay on one level.*

*KEY WORDS: Colobines – Cercopithecines – Enamel thickness – Molars – Folivory*

## INTRODUCTION

It is generally accepted that the two subfamilies of the Old World monkeys have different diets. The Colobinae are usually described as folivores, whereas the Cercopithecinae predominantly feed on fruit and other items (Fleage 1999).

Shellis and Hiiemae (1986) found that colobine lower incisors show a substantial layer of enamel on both the lingual and the labial aspect which result in blunt incisal edges, while cercopithecine incisors have no or little enamel on the lingual aspect. They concluded that this was correlated with the diet of the species studied.

Variation of enamel thickness on teeth between species with different diets can therefore be regarded as responses to functional demands through dietary specialization (Macho, Berner 1993, 1994). While the incisors grasp and cut food, the molars further process the solids (Kay, Covert 1984, Kay, Hylander 1978, Martin 1990). For the bilophodont molars of the Colobinae and Cercopithecinae, Kay and Hylander (1978) showed significant differences in the sharpness and length of the shearing blades, the cusps and the size of the crushing basins, clearly correlating with fruit- and leaf-eating. Therefore, differences in enamel thickness in molars are to be expected. Many authors already stated that colobine molars show thicker enamel than do cercopithecine molars, without testing this hypothesis on a sample of considerable size (e.g. Kay 1981).

This study wants to fill this gap and test this hypothesis on a sample of different species of Colobinae and Cercopithecinae. For determining enamel thickness, there exist various measures. Shellis *et al.* (1998, p. 508) state that "if the objective is inter-specific comparison, measures based on areas are to be preferred, since they are less influenced by variation in tooth shape and enamel distribution." The distribution of the enamel over the tooth depends on the different functional demands laid upon different regions. The inclusion of this aspect of enamel thickness helps to differentiate between groups with only slight differences in their diet. This can be of importance for this study, because the Colobines are not all specialized leaf-eaters, but rather include other items in their diet that differ between the species (Lucas, Teaford 1994, Martin 1990). Therefore, both the areas and the enamel thickness of different regions of the crown are included in this study (see below).

## MATERIAL AND METHODS

The study was based on 55 maxillary second molars from three cercopithecine and three colobine species (*Table 1*). The teeth were extracted from mostly subadult individuals from a collection of 379 cercopithecine and colobine crania. The teeth showed no or only minimal wear without the dentine being exposed.

TABLE 1. Composition of the sample.

| | Species | n |
|---|---|---|
| *Colobus* | *C. p. polykomos* | 13 |
| | *P. b. badius* | 8 |
| | *P. verus* | 2 |
| | | = 23 |
| *Cercopithecus* | *C. c. campbelli* | 25 |
| | *C. p. büttikoferi* | 5 |
| | *C. d. diana* | 2 |
| | | = 32 |

Prior to sectioning, the teeth were embedded in Technovitâ, to prevent damages to the enamel through sectioning. The teeth were then sectioned bucco-lingually, through the tips of the mesial cusps, and perpendicular to the base of the crown. In cases where the tips of the dentine cusps were not cut precisely, the tooth was ground down to the optimum plane.

The cut faces were transmitted to a computer by the image processing system VIDAS (KONTRON), taken by a video camera through a binocular. The tooth was fastened under a slide which was mounted on a device ensuring a standardized distance from the camera. Measurements were then taken on the digitalized pictures on the computer screen, using the software "scion-image", provided by the National Institute of Health.

Measurements from slightly worn areas were taken from the reconstructed original profile, and coded as missing values when the reconstruction was impossible. To minimize the error in measurement, the teeth were measured three times and the mean considered to correspond to the actual value.

Figure 1b lists the eleven measurements of enamel thickness taken for each tooth, recorded in mm. *Lt*, *Gt*, and *Ot* are taken perpendicular to the dentino-enamel junction, *Ft*, *Ch(l)* and *Ch(b)* perpendicular to the line which parallels the crown base through the deepest point of the enamel cap. Measurements *Lt(l), Gt(l), Ct(l), Ot(l), Ft, Ot(b), Ct(b), and Lt(b)* correspond to the variables 1–8 (Macho, Berner 1993), *Ch(l)* and *Ch(b)* to *H1* and *H2* (Macho, Berner 1994).

Additionally, measurements of areas and the length of the dentino-enamel junction were recorded (*Figure 1a*). These correspond to those applied by Martin (1983, 1985). To minimize the influence of tooth-size on these variables, some indices were calculated according to Martin (1983, 1985). First of all, the enamel cap area expressed as a percentage of dentine area was calculated: *Rea = (Ea / Da)* × 100. "Average enamel thickness" is defined as the area of the enamel cap divided by the length of the dentino-enamel junction: *Aet = Ea / Dej*. For "relative enamel thickness", Martin gives two different definitions. One possibility is dividing the root of the enamel area by the length of the dentino-enamel junction and multiplying by

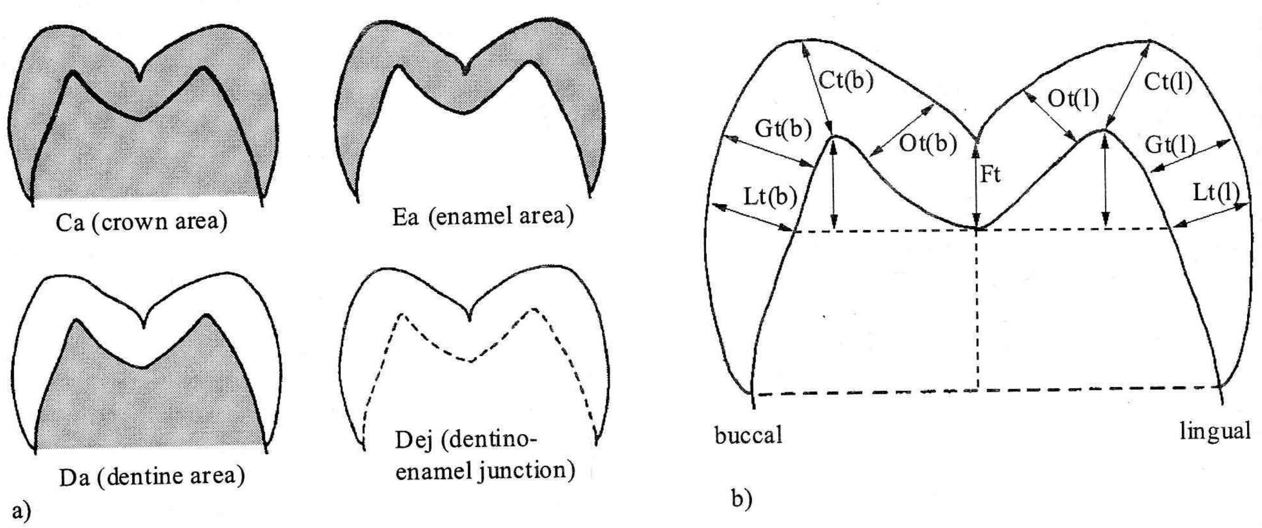



FIGURE 1. Cross-section through molar showing enamel thickness measures used in this study: a) variables of areas and the length of the dentino-enamel junction (DEJ), b) linear variables.





TABLE 2. Descriptive statistics.

| Measurement | | sample | Cercopithecines | Colobines | t | p |
|---|---|---|---|---|---|---|
| Lt(l) | N | 55 | 30 | 25 | –0.850 | 0.39 |
| | X | 0.59 | 0.5989 | 0.5764 | | |
| | SD | 0.01 | 0.0085 | 0.1113 | | |
| | min-max | 0.40–0.88 | 0.44–0.84 | 0.40–0.88 | | |
| Gt(l) | N | 54 | 30 | 24 | –2.531 | **0.016** |
| | X | 0.68 | 0.71 | 0.64 | | |
| | SD | 0.01 | 0.01 | 0.12 | | |
| | min-max | 0.43–0.94 | 0.57–0.84 | 0.43–0.94 | | |
| Ct(l) | N | 31 | 19 | 12 | 1.471 | 0.152 |
| | X | 0.64 | 0.60 | 0.71 | | |
| | SD | 0.21 | 0.14 | 0.28 | | |
| | min-max | 0.38–1.49 | 0.38–0.86 | 0.48–1.49 | | |
| Ot(l) | N | 54 | 30 | 24 | –0.508 | 0.614 |
| | X | 0.62 | 0.63 | 0.61 | | |
| | SD | 0.12 | 0.13 | 0.10 | | |
| | min-max | 0.37–0.87 | 0.37–0.37 | 0.44–0.81 | | |
| Ft | N | 55 | 30 | 25 | 2.162 | **0.035** |
| | X | 0.73 | 0.69 | 0.78 | | |
| | SD | 0.15 | 0.15 | 0.14 | | |
| | min-max | 0.43–1.04 | 0.43–1.02 | 0.48–1.04 | | |
| Ot(b) | N | 55 | 30 | 25 | 2.091 | **0.041** |
| | X | 0.58 | 0.55 | 0.61 | | |
| | SD | 0.11 | 0.11 | 0.12 | | |
| | min-max | 0.34–0.85 | 0.34–0.85 | 0.34–0.85 | | |
| Ct(b) | N | 39 | 22 | 17 | 1.004 | 0.322 |
| | X | 0.55 | 0.52 | 0.60 | | |
| | SD | 0.23 | 0.18 | 0.29 | | |
| | min-max | 0.32–1.59 | 0.33–0.98 | 0.32–1.59 | | |
| Gt(b) | N | 55 | 30 | 25 | 3.404 | **0.001** |
| | X | 0.54 | 0.50 | 0.59 | | |
| | SD | 0.01 | 0.01 | 0.01 | | |
| | min-max | 0.35–0.83 | 0.35–0.73 | 0.43–0.83 | | |
| Lt(b) | N | 55 | 30 | 25 | 5.592 | **0.000** |
| | X | 0.47 | 0.41 | 0.55 | | |
| | SD | 0.12 | 0.01 | 0.10 | | |
| | min-max | 0.26–0.79 | 0.26–0.61 | 0.36–0.79 | | |
| Ch(l) | N | 55 | 30 | 25 | 4.197 | **0.000** |
| | X | 1.28 | 1.17 | 1.41 | | |
| | SD | 0.25 | 0.21 | 0.22 | | |
| | min-max | 0.71–1.85 | 0.71–1.55 | 1.05–1.85 | | |
| Ch(b) | N | 55 | 30 | 25 | 1.606 | 0.114 |
| | X | 1.49 | 1.45 | 1.54 | | |
| | SD | 0.23 | 0.21 | 0.24 | | |
| | min-max | 0.85–2.10 | 0.85–1.80 | 0.99–2.10 | | |
| Ca | N | 55 | 30 | 25 | 9.354 | **0.000** |
| | X | 21.35 | 17.24 | 26.27 | | |
| | SD | 5.66 | 2.46 | 4.28 | | |
| | min-max | 12.53–32.43 | 12.53–23.42 | 14.09–32.43 | | |
| Da | N | 55 | 30 | 25 | 9.214 | **0.000** |
| | X | 14.96 | 11.76 | 18.81 | | |
| | SD | 4.52 | 2.16 | 3.46 | | |
| | min-max | 7.58–23.40 | 7.58–17.51 | 9.82–23.40 | | |
| Dej | N | 55 | 30 | 25 | 7.828 | **0.000** |
| | X | 12.84 | 11.73 | 14.16 | | |
| | SD | 1.67 | 1.08 | 1.23 | | |
| | min-max | 9.66–16.26 | 9.66–13.58 | 10.41–16.26 | | |
| Ea | N | 55 | 30 | 25 | 7.152 | **0.000** |
| | X | 6.38 | 5.48 | 7.47 | | |
| | SD | 1.38 | 0.57 | 1.29 | | |
| | min-max | 4.26–9.64 | 4.66–6.91 | 4.26–9.64 | | |
| Aet | N | 55 | 30 | 25 | 3.038 | **0.004** |
| | X | 0.50 | 0.47 | 0.53 | | |
| | SD | 0.01 | 0.01 | 0.01 | | |
| | min-max | 0.36–0.73 | 0.36–0.59 | 0.41–0.73 | | |
| Rea | N | 55 | 30 | 25 | –3.577 | **0.001** |
| | X | 30.55 | 32.15 | 28.61 | | |
| | SD | 4.03 | 3.69 | 3.61 | | |
| | min-max | 23.55–39.72 | 24.80–39.59 | 23.55–39.72 | | |
| Ret1 | N | 55 | 30 | 25 | –1.687 | 0.097 |
| | X | 19.71 | 20.06 | 19.28 | | |
| | SD | 1.73 | 1.72 | 1.69 | | |
| | min-max | 16.43–24.44 | 16.43–24.44 | 16.87–23.93 | | |
| Ret2 | N | 55 | 30 | 25 | –2.589 | **0.012** |
| | X | 13.19 | 13.92 | 12.31 | | |
| | SD | 2.41 | 2.33 | 2.24 | | |
| | min-max | 9.44–19.48 | 9.44–19.46 | 9.56–19.48 | | |

TABLE 3. Student's t-test for differences between lingual and buccal measures.

| Measurements | mean | SD | t | p |
|---|---|---|---|---|
| | | **Cercopithecinae** | | |
| Lt(l)-Lt(b) | 0.60 | 0.01 | 8.923 | **0.000** |
| | 0.41 | 0.01 | | |
| Gt(l)-Gt(b) | 0.71 | 0.01 | 13.326 | **0.000** |
| | 0.50 | 0.01 | | |
| Ct(l)-Ct(b) | 0.59 | 0.14 | 1.047 | 0.311 |
| | 0.55 | 0.19 | | |
| Ot(l)-Ot(b) | 0.63 | 0.13 | 3.788 | **0.001** |
| | 0.55 | 0.11 | | |
| | | **Colobinae** | | |
| **Measurements** | **mean** | **SD** | **t** | **p** |
| Lt(l)-Lt(b) | 0.58 | 0.11 | 2.114 | **0.045** |
| | 0.55 | 0.01 | | |
| Gt(l)-Gt(b) | 0.64 | 0.12 | 3.724 | **0.001** |
| | 0.59 | 0.01 | | |
| Ct(l)-Ct(b) | 0.74 | 0.35 | -0.485 | 0.645 |
| | 0.75 | 0.39 | | |
| Ot(l)-Ot(b) | 0.61 | 0.10 | -0.671 | 0.509 |
| | 0.62 | 0.10 | | |

100: $Retl = (\sqrt{Ea} / Dej) \times 100$. The other definition combines average enamel thickness with the dentine-component of the crown: $Ret2 = (Ea / Dej \times 100) / \sqrt{Da}$. In this study, both indices were calculated.

The recorded measurements were analysed statistically. Uni- and multivariate statistics were carried out using the SPSS statistical programme. The two sexes were analysed together because it was not possible to sex the subadult individuals.

## RESULTS

Descriptive statistics of all measurements and indices for the genera are given in *Table 2*. The colobine group shows a much greater intrageneric variability for almost all linear measures than do the Cercopithecines. The mean values for almost all absolute measures are greater in the Colobines, but not for the relative enamel thickness and some lingual measures. Comparisons of the measurements by Student's t-test show significant differences at the 5% level for all area measurements and two indices, but only some of the linear measurements.

Comparing not only the genera, but all the six species, the ANOVA gives similar results. Differences can mainly be observed for area measurements. These differences exist between species of differing body-size, but not e.g. between the two "big" colobine species, *C. polykomos* and *P. badius*, or the similar sized *C. campbelli* and *P. verus*.

Both, the Colobinae and the Cercopithecinae, have greater values for the lingual measurements than for the corresponding buccal ones. *Table 3* shows that for the Cercopithecines, all lingual measures but the cuspal thickness are significantly different from the buccal measures, but for the Colobines, only the lateral enamel layer differs significantly between the two aspects.

TABLE 4. Coefficients of the Principal Components (> 0.50).

| Measurement | I | II | III | IV |
|---|---|---|---|---|
| | | **Principal Component** | | |
| Lt(l) | | | 0.902 | |
| Gt(l) | | | 0.852 | |
| Ct(l) | | 0.627 | | |
| Ot(l) | | | | 0.785 |
| Ft | | | | 0.872 |
| Ot(b) | | | | 0.716 |
| Ct(b) | | 0.884 | | |
| Gt(b) | 0.683 | | | |
| Lt(b) | 0.803 | | | |
| Ch(l) | | | −0.558 | |
| Ch(b) | | −0.750 | | |
| Ca | 0.953 | | | |
| Da | 0.925 | | | |
| Dej | 0.852 | | | |
| Ea | 0.880 | | | |
| Aet | | 0.600 | | |
| Rea | | 0.600 | | |
| Ret1 | | 0.774 | | |
| Ret2 | | 0.726 | | |

Principal Components Analysis (PCA) was carried out in order to explore structural connections between the different measures applied (*Table 4*). The first principal component (PC I) is associated with the measures which are correlated with the overall tooth-size and accounts for about 30% of the variance. PC II, which accounts for 23% of the variance, reveals connections between the relative measures, the enamel thickness on the cusps and the height of the buccal dentine cusp. PC III summarizes the lingual, and PC IV the occlusal linear measures. Plotted against each other (*Figure 2*), the principal components reveal that Colobines and Cercopithecines can be separated by the first principal component only. This corresponds with the results of the ANOVA. Concerning possible allometrical effects see discussion below.





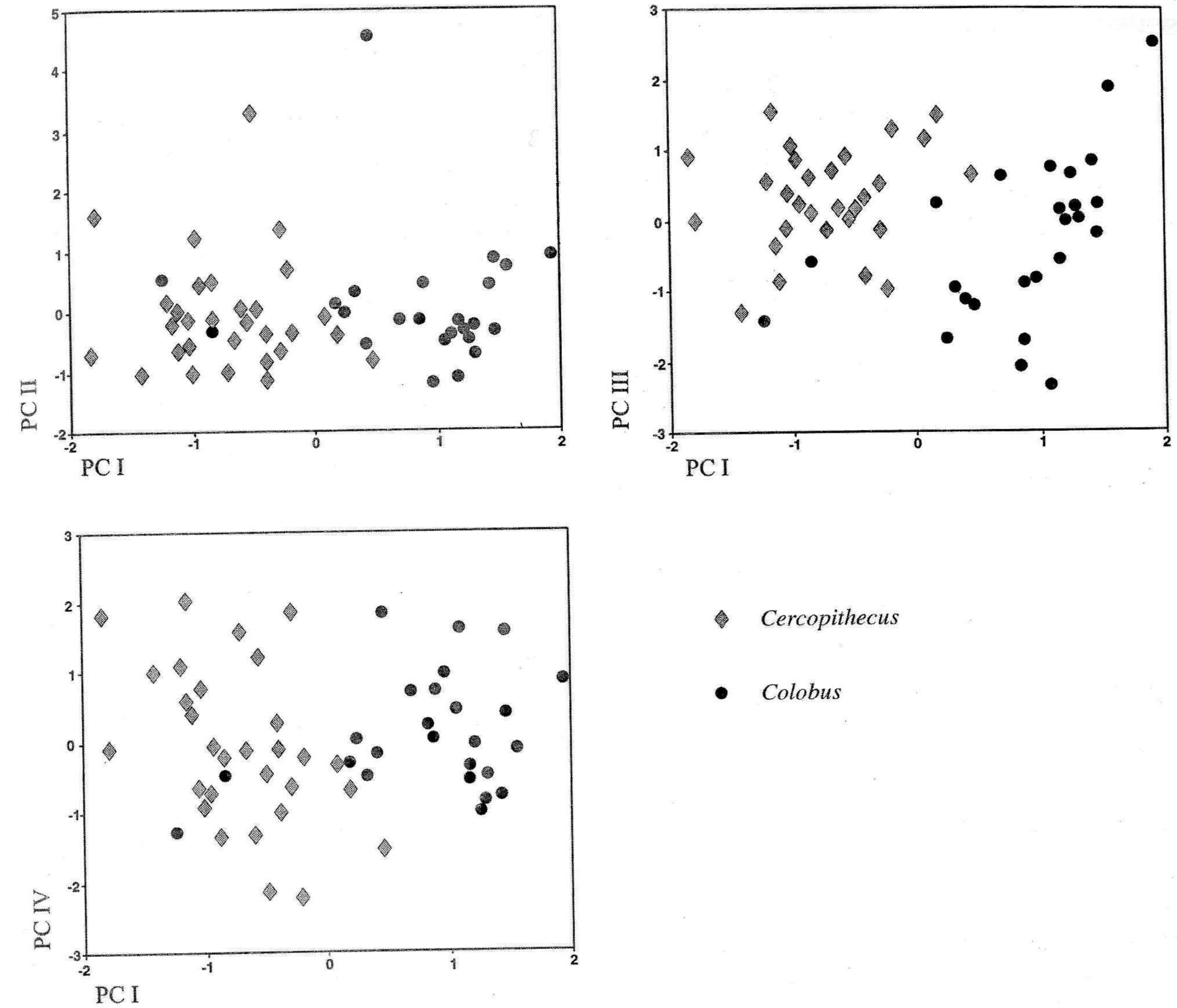
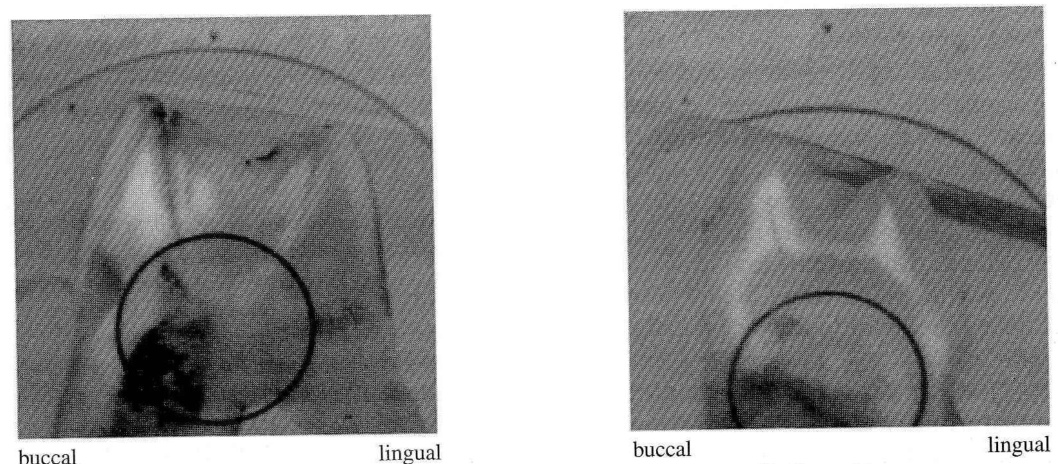



FIGURE 2. Plot of principal components I and II, I and III, and I and IV.




a) *Colobus*   b) *Cercopithecus*

FIGURE 3. Cross section through a) colobine and b) cercopithecine maxillary molar.

## DISCUSSION AND CONCLUSION

By statistical analysis, there can be described some differences between colobine and cercopithecine molar enamel thickness that could be related to their dietary specializations.

As in all primate maxillary molars, the enamel layer on the lingual side is thicker than on the buccal aspect. This can be explained by the greater masticatory stress on the lingual side of maxillary molars (Grine, Martin 1988, Macho, Berner 1993, Macho, Thackeray 1992, Molnar, Gantt 1977, Molnar, Ward 1977). Within the Colobines, there are no significant differences on the occlusal aspect, but they have significantly thicker enamel than the Cercopithecines on the buccal, but thinner enamel on the lingual side. Therefore in colobine maxillary molars, the difference between the lingual and the buccal enamel thickness is less than in cercopithecine teeth. This can also be seen in direct comparison of the tooth sections (*Figure 3*). The function of this pattern of enamel distribution may be in the uniform abrasion of the enamel on both cusps, so that the shearing blades for shearing the fibers of the leaves lay on the same level.

The greater enamel thickness on the occlusal plane in colobine teeth is indicating greater masticatory stress on this region. Happel's (1988) interpretation of the central basin of bilophodont molars as "mortar" can be proven by this observation. This structure cannot be connected to a fibrous diet and must therefore reflect the adaptation on other items of the colobine diet like seeds. A better interpretation of the functional demands on these different regions could maybe be obtained from microwear analysis.

For this comparison, the absolute measurements were used that were strongly influenced by tooth-size, so that the result must be viewed very cautiously. To be able to compare the species directly, indices according to Martin (1983, 1985) were obtained. For some of these, the Colobines showed significantly thinner enamel than the Cercopithecines. Nevertheless, the genera could not be separated by their relative enamel thickness. This is in accordance with the observations of Macho (1994), Macho and Berner (1993), and Shellis *et al.* (1998), who found that these indices defined by Martin rather conceal differences in enamel thickness, because the formula are based on isometry between tooth- and body-size, but there is allometry. Other indices that take the allometry into consideration should reinforce the observation that colobine molars have relatively thinner enamel than cercopithecine teeth. So the hypothesis that the folivorous Colobinae have thinner enamel than the fruit-eating Cercopithecinae can be confirmed. But this holds true only when *relative* enamel thickness is regarded.

Because of the weakness of the indices, the measurements that are influenced by tooth-size formed the first principal component that accounted for 30 % of the variation and was the most powerful in separating the genera. But the second principal component is worth looking at nonetheless. Here, the relative measures are positively correlated to the enamel thickness on the cusps, but negatively to the height of the dentine cusps. This means that the higher the cusps, the thinner the enamel on the tooth. Through this observation, the hypothesis that the relatively thin enamel of the colobine molars is caused by the leaf-eating of the species can be suggested intensively, if we take the observations of Kay (1975, 1978) and Kay and Hylander (1978), concerning the correlation of high cusps with folivory, into account.

Because of the inability to overcome the problems of comparing teeth of different sizes, it was not possible to find intrageneric differences between the species of Colobinae and Cercopithecinae, respectively. Comparing the enamel thickness and enamel distribution of species that differ only in some aspects of their diet may give further insight into the functional demands that are laid upon special regions of the molar crown by different foods – a task to be solved in the future.

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## REFERENCES

FLEAGLE J.G., 1999: *Primate Adaptation and Evolution.* 2nd Edition. Academic Press, London.

GRINE F. E., MARTIN L. B., 1988: Enamel Thickness and Development in *Australopithecus* and *Paranthropus*. In: F. E. Grine (Ed.): *Evolutionary History of the "Robust" Australopithecines.* Pp. 3–42. A. de Gruyter, New York.

HAPPEL R., 1988: Seed-eating by West African Cercopithecines, with reference to the possible evolution of bilophodont molars. *Amer. J. of Phys. Anthrop.* 75: 303–327.

KAY R. F., 1981: The Nut-Crackers – a new theory of the adaptations of the Ramapithecinae. *Amer. J. Phys. of Anthrop.* 55: 141–151.

KAY R. F., COVERT H. H., 1984: Anatomy and behaviour of extinct primates. In: D. J. Chivers, A. Bilsborough (Eds.): *Food acquisition and processing in primates.* Pp. 467–508. Plenum Press, New York.

KAY R. F., HYLANDER W. L., 1978: The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). In: G. G. Montgomery (Ed.): *The Ecology of arboreal folivores.* Pp. 173–191. Smithsonian Institute Press, Washington D.C.

LUCAS P. W., TEAFORD M. F., 1994: Functional morphology of colobine teeth. In: A. G. Davies, J. F. Oates (Eds.): *Colobine monkeys: their ecology, behaviour and evolution.* Pp. 173–203. Cambridge University Press, Cambridge.





MACHO G. A., 1994: Variation in enamel thickness and cusp area within human maxillary molars and its bearing on scaling techniques used for studies of enamel thickness between species. *Arch. oral Biol.* 39: 783–792.

MACHO G. A., BERNER M. E., 1993: Enamel thickness of human maxillary molars reconsidered. *Amer. J. of Phys. Anthrop.* 92: 189–200.

MACHO G. A., BERNER M. E., 1994: Enamel thickness and the helicoidal occlusal plane. *Amer. J. of Phys. Anthrop.* 94: 327–337.

MARTIN L. B., 1983: The relationships of the Later Miocene hominoidea. Ph.D. Thesis, Univ. of London.

MACHO G. A., THACKERAY, J. F., 1992: Computed tomography and enamel thickness of maxillary molars of Plio-Pleistocene hominids from Sterkfontein, Swartkrans, and Kromdraai (South Africa): an exploratory study. *Amer. J. of Phys. Anthrop.* 89: 133–143.

MARTIN L. B., 1985: Significance of enamel thickness in hominoid evolution. *Nature* 314: 260–263.

MARTIN R. D., 1990: *Primate origins and evolution: a phylogenetic reconstruction.* Chapman and Hall, London.

MOLNAR S., GANTT, D. G., 1977: Functional implications of primate enamel thickness. *Amer. J. of Phys. Anthrop.* 46: 447–454.

MOLNAR S., WARD S. C., 1977: On the hominid masticatory complex: biomechanical and evolutionary perspectives. *J. of Hum. Evol.* 6: 557–568.

NAPIER J. R., NAPIER P. H., 1967: *A handbook of living primates: morphology, ecology and behaviour of nonhuman primates.* Academic Press, London

SHELLIS R. P., HIIEMAE K. M., 1986: Distribution of enamel on the incisors of old World monkeys. *Amer. J. of Phys. Anthrop.* 71: 103–113.

SHELLIS R. P., BEYNON A. D., REID D. J., HIIEMAE K. M., 1998: Variation in molar enamel thickness among primates. *J. of Hum. Evol.* 35: 507–522.

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