Scanning Microscopy Vol. 10, No. 2, 1996 (pages 349-370) 0892-953X/96$5.00+.25
Scanning Microscopy International, Chicago (AMF O'Hare), IL 60666 USA

# ENAMEL PRISM MORPHOLOGY IN MOLAR TEETH OF SMALL EUTHERIAN MAMMALS

Elizabeth R. Dumont*

Department of Anthropology, SUNY at Stony Brook, Stony Brook, New York 11794

(Received for publication June 9, 1995 and in revised form November 12, 1995)

## Abstract

Data summarizing enamel prism shape, size and spacing are reported for the molar enamel of 55 species of small eutherian mammals including primates, bats, tree shrews, flying lemurs, insectivorans and representatives of a variety of fossil families. Confocal photomicrographs reveal that the subsurface enamel of most species is characterized by arc-shaped prisms. The lack of a clear distinction between pattern 2 and pattern 3 prism configurations within single specimens suggests that the broad category "arc-shaped prisms" is the most appropriate descriptive grouping for these species. Of the total sample, three species exhibit only circular prisms while no evidence of prismatic enamel was found in two bats. Prism shape is not an informative phylogenetic character at the ordinal level for these morphologically primitive and relatively thin-enameled taxa. Significant differences between species in several prism size and spacing variables (central distance between prisms, prism diameter, prism area and the ratio of prism area to estimated ameloblast area) suggest the potential for further analyses of quantitative variation to document evolutionary relationships within or among family-level groups.

**Key Words:** Mammals, enamel prisms, variation, prism patterns, evolution.

*Address for correspondence and current address:
Elizabeth R. Dumont
Department of Anatomy,
Northeastern Ohio Universities College of Medicine,
4209 State Route 44, P.O. Box 95,
Rootstown, OH 44272
Telephone number: (330) 325-2511
FAX number: (330) 325-2524

## Introduction

The microstructural morphology of tooth enamel has recently emerged as a useful tool in investigating evolutionary relationships among mammals. Evolutionary analyses have focussed on the phylogenetic significance of aspects of enamel microstructure ranging from the size, shape and spacing of enamel prisms to the relationship of enamel prisms to one another as they as they pass from the enamel-dentine junction to the outer tooth surface. Enamel morphology is well-documented in multituberculates (Fosse *et al.*, 1978, 1985; Sahni, 1979; Carlson and Krause, 1985; Krause and Carlson, 1986, 1987), marsupials (Boyde and Lester, 1984; Lester *et al.*, 1987, 1988) and selected eutherian groups including primates (Boyde and Martin, 1982, 1984a, 1984b; Grine *et al.*, 1986; Martin *et al.*, 1988; Maas, 1993, 1994), and rodents (Wahlert, 1968; Boyde, 1978; Wahlert and von Koenigswald, 1985). While these studies represent significant contributions to our knowledge of the range of enamel morphology among mammals, there are many mammalian taxa whose enamel structure is currently unknown.

Enamel prism boundaries are formed by discontinuities surrounding similarly oriented groups of hydroxyapatite crystals. In most mammals, prisms span much of the distance between the enamel-dentine junction and outer surface of the tooth. Boyde (1964, 1969) defined three distinct prism patterns on the basis of prism cross sectional shape, size and spatial organization as determined from developing enamel surfaces (Fig. 1). Subsequently, Fosse (1968a,b,c,d,e) developed a series of measurements designed to quantify cross-sectional prism size and spacing. The combination of qualitative and quantitative data summarizing enamel prism shape, size and spacing has proven useful in interpreting the evolution of multituberculate mammals (Carlson and Krause, 1985; Krause and Carlson, 1986, 1987).

This study presents a survey of cross-sectional enamel prism morphology within the molar teeth of a broad range of small eutherian mammals. Qualitative and quantitative data summarizing the cross sectional

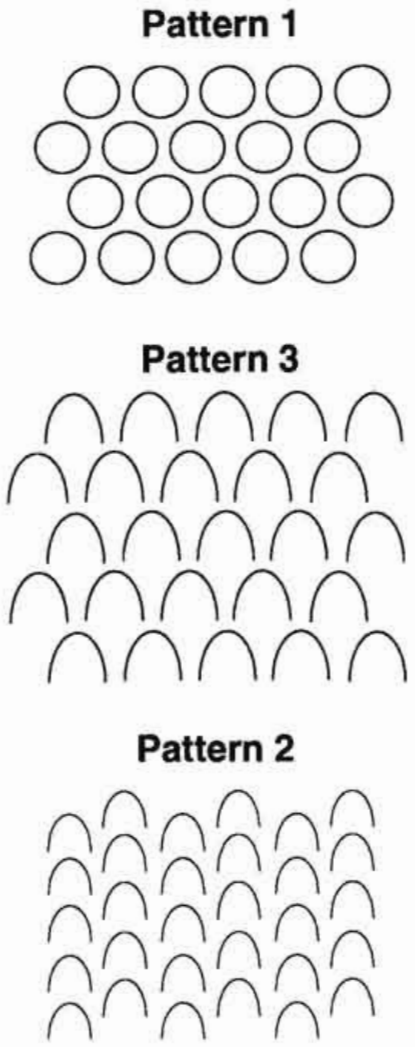



**Figure 1.** Diagram illustrating enamel prism patterns 1, 3 and 2. Each pattern exhibits a unique combination of enamel prism shape, size and spatial distribution. Solid lines represent the boundaries of prisms sectioned perpendicular to their long axes. The apex of the tooth is toward the top of the page.

---

morphology of molar tooth enamel from a variety of living primates, tree shrews (Order Scandentia), bats (Order Chiroptera), insectivorans (Order Lipotyphla), elephant shrews (Order Macroscelidea) and the flying lemur (Order Dermoptera) is presented. Enamel prism morphology is also summarized for the fossil families Plesiadapidae, Paromomyidae, Microsyopidae, Leptictidae and Mixodectidae, which have been suggested to be allied with one or more living mammalian orders.

## Methods

Enamel from 125 individuals encompassing 55 species, 26 families and at least seven mammalian orders

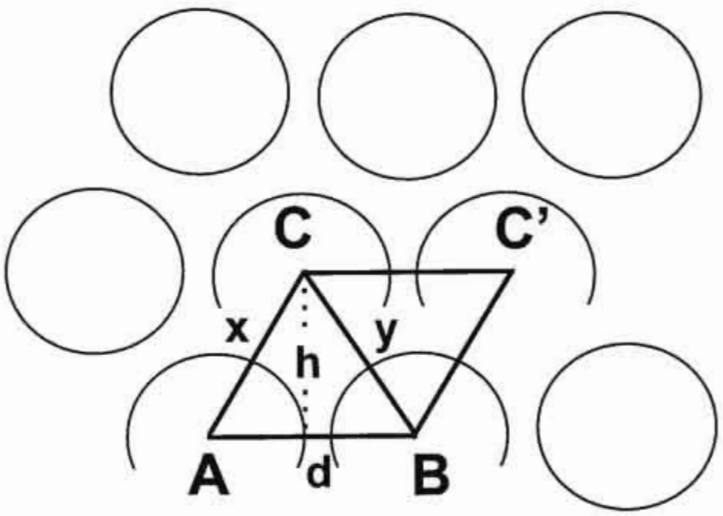



**Figure 2.** The two dimensional model of prism patterns 1 and 3 used to calculate the central distance between prisms and estimated ameloblast area. Formulae for these calculations are given in Fosse (1968a,b,c,d,e). (Figure after Grine *et al.*, 1986).

---

was sampled (Table 1). Where possible, cross-sectional enamel prism morphology was examined on the buccal aspect of the lower first molar protoconid, the most primitive and first-formed cusp (Butler, 1941, 1956). The enamel of whole, unsectioned teeth were investigated using confocal microscopy {Tracor® (Noran Instruments, Middleton, WI), Tungsten light source, 50X oil immersion objective} and images were recorded on 35 mm film (Tmax®, ASA 400; Eastman Kodak Co., Rochester, NY).

Using confocal microscopy, the opacity of the specimen and the working distance of the lens are the sole factors limiting the depth from which images can be acquired. In the present study, the enamel of each specimen was surveyed from several locations as deep within the specimen as possible. Both qualitative and quantitative assessments of enamel structure are based on the deepest available sections and most consistent enamel morphologies. Between one and eight photomicrographs ($\bar{x}$ = 2.7) of each specimen were examined to discern the shape and spatial distribution of enamel prisms. The mean and standard error of depth values for each specimen are reported in Table 1.

To assess quantitative variability in prism size and distribution among species, a sample of 10 measurements each of prism area (pa), prism diameter (pd), the average distance between prism centers (cd) and estimated ameloblast area (aa) was collected from each photomicrograph. Central distance and ameloblast area were calculated following the method developed by Fosse (1968a,b,c,d,e) that uses a series of line segments

**For Micrographs and Tables:** Key to museum acronyms: American Museum of Natural History (AMNH); Academy of Natural Sciences (ANSP); Carnegie Museum of Natural History (CM); Department of Zoology, University of Michigan (DZUM); Florida State Museum (FSM); Field Museum of Natural History (FMNH); Museum of Vertebrate Zoology (MVZ); Yale Peabody Museum, Princeton Collection (YPM-PU); Rijksmuseum Van Natuurlijke Historie (RVNH); State University of New York at Stony Brook (SUSB); Texas Tech University (TT); University of Alberta (UA); University of Michigan Museum of Paleontology (UM); and U.S. Geological Survey (USGS).

---

drawn between the centers of adjacent prisms (Fig. 2). Prism diameter (measured perpendicular to the apicocervical axis of the tooth) and prism area were measured directly from enlarged photomicrographs. For each micrograph, a sample of ten prism to estimated ameloblast area (pa/aa) values was calculated by randomly combining the ten prism end estimated ameloblast area measurements.

Prism size and spacing measurements were made from tracings of projected negatives. To insure uniform magnification among the photomicrographs, all enlargement factors, i.e., objective and magnifying lenses in both the microscope and negative projection apparatus, were held constant. Absolute scale was determined using a photomicrograph of a micrometer taken using the identical microscope configuration and negative projection procedures used for the enamel photomicrographs. All measurements were calibrated using this scale.

Mean values summarizing the average central distance between prisms, prism cross-sectional area, estimated ameloblast area, and an estimate of the area of interprismatic enamel was calculated for each specimen using all available measurements. The presences of significant differences in these parameters between species was investigated using the non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1981). Eleven specimens of the microchiropteran bat *Taphozous mauritianus* were collected to investigate the consistency of qualitative assessments of enamel prism morphology within species.

## Results

An external layer of prism-free enamel was characteristic of virtually all specimens. This layer was typically underlain by circular prisms that most often gave way to a deeper layer of arc-shaped prisms. Qualitative assessments of the deepest available enamel for each species are provided below. With the exception of some

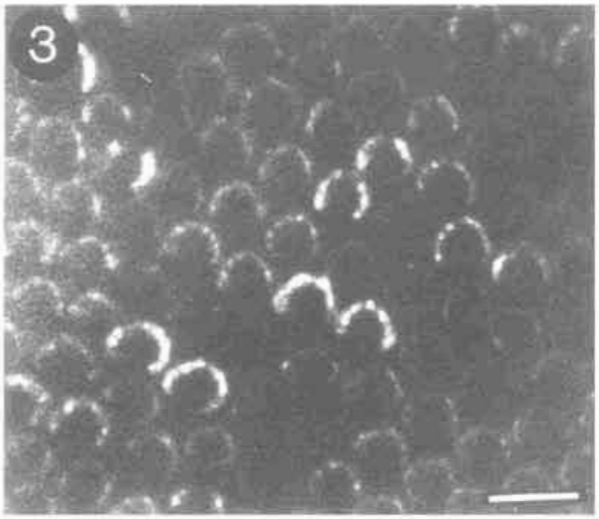



**Figure 3.** The enamel of *Notharctus* sp. (CM 34485) taken at a depth of 50 $\mu$m below the buccal surface of the right m1 protoconid. Bar = 5 $\mu$m.

---

of the larger taxa (*Erinaceus europaeus*, *Chiromyoides* sp., *Plesiadapis (P.) rex*, *Plesiadapis (P.) cookei*), prisms appear to follow a relatively straight path from the outer surface of the tooth toward the enamel-dentine junction, i.e., there was no evidence of prism decussation. Although the presence of decussating enamel has been documented in *Lemur* using scanning electron microscopy (SEM) (Maas, 1994), it was not visible using the confocal microscopy techniques employed here.

Quantitative data summarizing pd, pa, cd and pa/aa values for each species are presented in Tables 2 and 3. These tables also report the results of a Kruskall-Wallis test performed on each variable. Each variable exhibits significant variation between species ($p < 0.002$).

### Order primates

Enamel was sampled from representatives of the families Adapidae, Omomyidae, Lemuridae, Galagidae and Tarsiidae. The notharctine adapids *Cantius* sp., *Cantius mckennai* and *Notharctus* sp. exhibit arc-shaped prisms that are most often organized into a pattern 3 arrangement (Figs. 3 and 4). The prism pattern of *Adapis parisiensis*, however, is markedly different. Confocal photomicrographs of *Adapis* enamel reveal prisms that are either completely closed (e.g., pattern 1) or prisms that are almost completely closed, but still arc-shaped (Fig. 5). Except for having smaller prisms, omomyid enamel resembles that of the notharctine adapids *Cantius* and *Notharctus*. Individuals of *Teilhardina americana*, *Tetonius* sp. and *Washakius insignis* possess small, arc-shaped pattern 3 prisms (Fig. 6).

**Table 1.** Specimens sampled using tandem scanning microscopy. Specimen number (Specimen), tooth position (Tooth), the area of enamel that was surveyed (Area) and the mean and standard error of the depth from which images were obtained (Depth, in $\mu$m) are reported; ent = entoconid; mtd = metaconid; prd = protoconid; hyd = hypoconid; buccal = buccal surface; lingual = lingual surface; pro = protocone; mci = mesial cingulum; bci = buccal cingulum. Dashes denote missing data.

| Taxon | Specimen | $N_m$ | Tooth | Area | Depth |
|---|---|---|---|---|---|
| **Order Primates** | | | | | |
| Suborder Strepsirhini | | | | | |
| Family Adapidae | | | | | |
| *Adapis pariesiensis* | CM 2563 | 3 | Lp3\m3 | prd/pad | 31 ± 9.5 |
| | CM 409 | 3 | Lm1 | ent | 27 ± 14.0 |
| *Cantius* sp. | SUSBuncat. | 4 | Rm1 | prd | 20 ± 6.5 |
| | CM uncat. | 1 | Mx | lingual | 33 |
| *Cantius mckennai* | CM 12139 | 3 | Rm1 | prd | 26 ± 2.3 |
| | CM 12163 | 3 | Lm1 | prd | 26 ± 6.4[2] |
| | CM 12267 | 3 | Lm1 | prd | -- |
| *Notharctus* sp. | CM 34485 | 3 | Rm1 | prd | 38 ± 12.5 |
| | CM 13920 | 3 | Rm2 | hyd | 45 ± 5.9 |
| | CM 53982 | 3 | Lm1 | prd | -- |
| Family Omomyidae | | | | | |
| *Teilhardina americana* | USGS 15406 | 3 | Rp4 | prd | 10 ± 0.6 |
| | USGS 7193 | 1 | Rm1 | prd | 30 |
| *Tetonius* sp. | USGS 5960 | 2 | Rm1 | met | 37 ± 24.0 |
| *Washakius insignis* | AMNH | 2 | Rm1 | prd | 19 ± 12.0 |
| Family Lemuridae | | | | | |
| *Lemur* sp. | SUSB uncat. | 2 | Lp4 | prd | 17 ± 2.1 |
| Family Galagidae | | | | | |
| *Galagoides demidovii* | SUSB81-17 | 3 | Rm1 | prd | 22 ± 2.5 |
| | SUSB Pga2 | 3 | Lm1 | prd | 22 ± 4.9 |
| Suborder *incerta sedis* | | | | | |
| Family Tarsiidae | | | | | |
| *Tarsius bancanus* | SUSBuncat. | 1 | Rm1 | prd | 10 |
| Order Scandentia | | | | | |
| Family Tupaiidae | | | | | |
| *Lyonogale tana* | AMNH 102831 | 3 | Rm1 | prd | 43 ± 2.8 |
| | AMNH 102830 | 3 | Rm1 | prd | 42 ± 2.9 |
| | AMNH 102829 | 3 | Rm1 | prd | 40 ± 0.0[2] |
| *Tupaia glis* | AMNH 26844 | 2 | Rm1 | hyd | 30 ± 1.4 |
| | AMNH 54788 | 3 | Rm1 | prd/hyd | 40 ± 13.8 |
| | SUSBuncat. | 4 | Rm1 | hyd | 34 ± 6.4 |
| *Urogale everetti* | AMNH 203290 | 3 | Rm1 | prd | 42 ± 9.9 |
| | AMNH 203291 | 3 | Rm1 | prd | 36 ± 6.5 |
| | AMNH 203292 | 3 | Rm1 | prd | 42 ± 5.9 |
| Order Dermoptera | | | | | |
| Family Cynocephalidae | | | | | |
| *Cynocephalus variegatus* | RVNH 14516 | 4 | Rm1 | prd | 26 ± 3.9 |
| | RVNH 12318 | 2 | Rm1 | prd | 33 ± 3.5 |
| | RVNH 15820 | 2 | Rm1 | prd | 28 ± 3.5 |
| | RVNH 12317 | 2 | Rm1 | prd | 32 ± 2.12 |

**Table 1 continued**

| Taxon | Specimen | $N_m$ | Tooth | Area | Depth |
|---|---|---|---|---|---|
| Order Chiroptera | | | | | |
| Suborder Microchiroptera | | | | | |
| Family Emballonuridae | | | | | |
| *Balantiopteryx plicata* | CM 38123 | 3 | Rm1 | prd | 29 ± 1.2 |
| | CM 38128 | 2 | Lm1 | prd | 20 ± 6.4 |
| | CM 38122 | 4 | Lm1 | prd | 18 ± 6.4 |
| | CM 38124 | 5 | Lm1 | prd | 22 ± 7.6 |
| *Taphozous mauritianus* | CM 84242 | 7 | Rm1 | prd | 13 ± 5.6[2] |
| | AMNH 48778 | 5 | Rm1 | hyd | 19 ± 5.6 |
| | AMNH 48777 | 3 | Rm1 | hyd | 25 ± 9.5 |
| | AMNH 48798 | 3 | Rm1 | hyd | 15 ± 3.2 |
| | AMNH 48776 | 3 | Rm1 | prd | 19 ± 7.1[2] |
| | AMNH 48806 | 3 | Rm1 | prd | 28 ± 8.7 |
| | AMNH 4807 | 3 | Rm1 | prd | 23 ± 6.8 |
| | AMNH 48805 | 3 | Rm1 | prd | 27 ± 5.6 |
| | AMNH 48800 | 3 | Rm1 | prd | 12 ± 2.5 |
| | AMNH 48794 | 3 | Rm1 | prd | 23 ± 10.6 |
| | AMNH 48804 | 3 | Rm1 | prd | 19 ± 5.2 |
| Family Rhinopomatidae | | | | | |
| *Rhinopoma hardwickei* | TT 40638 | 8 | Lm2/Rm1 | prd | 11 ± 2.4 |
| Suborder Megachiroptera | | | | | |
| Family Pteropodidae | | | | | |
| *Pteropus insularis* | AMNH 249956 | 3 | Rm1 | prd | 16 ± 8.0 |
| | AMNH 249958 | 3 | Rp4 | prd | 19 ± 0.7[2] |
| | AMNH 249961 | 3 | Rm1 | prd | 11 ± 1.5 |
| | AMNH 249962 | 2 | Rm1 | prd | -- |
| *Rousettus amplexicaudatus* | MVZ 141114 | 3 | Lm1 | prd | 15 ± 3.5 |
| | MVZ 141116 | 3 | Lm1 | prd | 15 ± 4.4 |
| | RVNH 28267 | 8 | Rm1 | prd | 16 ± 7.3 |
| *Nyctimene albiventor*[1] | MVZ 3149 | - | Rm1 | prd | -- |
| | MVZ 138513 | - | Rm1 | prd | -- |
| | MVZ 138514 | - | Rm1 | prd | -- |
| *Paranyctimene raptor*[1] | MVZ 140312 | - | Rm1 | prd | -- |
| | MVZ 140310 | - | Rm1 | prd | -- |
| Order *incerta sedis* | | | | | |
| Suborder Plesiadapiformes | | | | | |
| Family Phenacolemuridae | | | | | |
| *Ignacius frugivorus* | CM 16264 | 2 | Rm1 | prd | 42 ± 6.4 |
| | CM 16296 | 3 | Rm1 | ent | 29 ± 4.9[2] |
| *Ignacius graybullianus* | UM 86538 | 5 | Rm1 | prd | 35 ± 7.9 |
| | UM 89978 | 3 | Lm3 | prd | 24 ± 7.2 |
| Family Plesiadapidae | | | | | |
| *Chiromyoides* sp. | UM 61534 | 3 | Rm1\m2 | prd | 35 ± 5.0 |
| *Nannodectes intermedius* | UM 83059 | 2 | Lm1 | prd | 26 ± 5.7 |
| *Plesiadapis cookei* | UM 63289 | 3 | Rm1\m2 | prd | 36 ± 2.9 |
| *Plesiadapis rex* | UM 64525 | 3 | Rm1 | prd | 22 ± 7.8 |
| | UM 870053 | 3 | Lm2 | prd | 19 ± 5.6[2] |
| | UM 870061 | 2 | Rm2 | prd | 21 ± 3.5 |

**Table 1 continued**

| Taxon | Specimen | $N_m$ | Tooth | Area | Depth |
|---|---|---|---|---|---|
| *Pronothodectes matthewi* | AMNH 9847 | 1 | Rm1 | prd | 23 |
| | AMNH 35467 | 2 | Rm1 | prd | 17 ± 0.0 |
| | AMNH 35468 | 2 | Rm1 | prd | 18 ± 0.7 |
| Family Microsyopidae | | | | | |
| *Cynodontomys* sp. | CM 41536 | 4 | Lm1 | prd | 37 ± 11.4 |
| | CM 38825 | 7 | Rm2 | prd | 31 ± 10.7 |
| *Microsyops angustidens* | UM 80861 | 5 | Rm1 | prd | 30 ± 7.9 |
| *Microsyops* sp. | CM uncat. | 3 | Rm1 | prd | 18 ± 6.4 |
| *Niptomomys doreeni* | USGS 81488 | 2 | Rm1 | prd | 28[2] |
| | USGS 25647 | 3 | Rm1 | prd | 16 ± 0.0[2] |
| Family Carpolestidae | | | | | |
| *Carpodaptes hazelae* | UM 89944 | 4 | Lp4 | buccal | 17 ± 4.4 |
| | UM 89943 | 3 | Lp4 | buccal | 21 ± 5.9 |
| *Elphidotarsius russelli* | YPM-PU | 1 | Rp4 | prd | 12 |
| Family Picrodontidae | | | | | |
| *Picrodus* sp. | UM 16578 | 1 | Lm1 | prd | 9 |
| | UM 19746 | 2 | Rm1 | prd | 15 ± 14.8 |
| Family Saxonellidae | | | | | |
| *Saxonella naylori* | UA 31494 | 2 | RP3 | prd | 12 ± 3.5 |
| Family *inserta sedis* | | | | | |
| *Purgatorius* sp. nov. | UM 860650 | 5 | Lm1 | prd | 26 ± 12.6 |
| | UM 860574 | 2 | Lm1 | prd | 19 ± 12.0 |
| Order Lipotyphla | | | | | |
| Family Erinaceiidae | | | | | |
| *Atelerix albiventris* | FSM 20551 | 6 | Rm1 | prd | 14 ± 5.6 |
| | FSM 20553 | 1 | Rm1 | prd | -- |
| | FSM 20552 | 1 | Rm1 | prd | 17 |
| *Erinaceus europaeus* | TT 49630 | 1 | Lm1 | prd | 32 |
| | TT 49634 | 2 | Rm1 | prd | 16 ± 2.1 |
| | MVZ 127969 | 3 | Rm1 | prd | 25 ± 4.2 |
| | MVZ 127970 | 3 | Rm1 | prd | 19 ± 4.6 |
| | MVZ 127971 | 1 | Rm1 | prd | 20 |
| Family Dormaalidae | | | | | |
| *Litocherus notissimus* | UM 89873 | 2 | Lm1 | prd | 16 ± 0.7 |
| | UM 89981 | 2 | Rm1 | prd | 17 ± 2.8 |
| | UM 89879 | 1 | Rm1 | prd | 9 |
| Order *incerta sedis* | | | | | |
| Family Apatemyidae | | | | | |
| *Apatemys* sp. | CM 36257 | 6 | Rm2 | prd | 45 ± 18.7 |
| | CM 38122 | 3 | Lm1 | prd | 32 ± 3.1 |
| *Labidolemur kayi* | UM 81474 | 3 | Rm1 | prd | 18 ± 4.5 |
| *Unuchinia asaphae* | UM 89931 | 4 | LI2 | buccal | 26 ± 5.4 |
| Family Leptictidae | | | | | |
| *Prodiacodon* | UM 84213 | 2 | Rp4 | prd | 33 ± 4.2 |
| *concordiarensis* | UM 84217 | 3 | Rmx | prd | 38 ± 7.6 |
| Family Mixodectidae | | | | | |
| *Eudaemonema cuspidata* | AMNH 35823 | 5 | Rp4 | prd | 23 ± 6.9 |
| *Mixodectes malariss* | AMNH 16604 | 4 | Rm1 | prd | 15 ± 4.8 |

**Table 1 continued**

| Taxon | Specimen | $N_m$ | Tooth | Area | Depth |
|---|---|---|---|---|---|
| Family Nyctitheridae | | | | | |
| *Leptacodon tener* | UM 84230 | 2 | Rm2 | prd | 13 ± 0.7 |
| | UM 84588 | 1 | Rm1 | prd | 30 |
| | UM 89607 | 3 | Rm1 | prd | -- |
| *Nyctitherium serotinum* | AMNH 12061 | 3 | Rm2 | lingual | 22 ± 3.5[2] |
| Family Palaeoryctidae | | | | | |
| *Palaeoryctes* sp. | UM 84207 | 3 | LM1\M2 | pro | 62 ± 11.6 |
| | UM 84206 | 2 | LM1 | pro | 30 ± 1.4 |
| Family Plagiomenidae | | | | | |
| *Elpidophorus elegans* | UM 89913 | 3 | Lm2 | prd | 23 ± 1.5 |
| | UM 89906 | 2 | Rm1\m2 | prd | 37 ± 2.8 |
| | UM 89911 | 1 | Lm1\m2 | prd | 38 |
| | UM 89905 | 1 | Lm1\m2 | prd | 17 |
| *Plagiomene multicuspis* | UM 73034 | 2 | Rmx | mci | 25 ± 1.4 |
| | UM 70-1044 | 2 | Rmx | bci | 18 ± 3.5 |
| *Planetetherium mirabile* | AMNH 22205 | 5 | Rm1 | prd | 22 ± 4.3[2] |
| *Worlandia inusitata* | UM 71040 | 3 | Lp3 | prd | 22 ± 4.2 |
| | UM 850758 | 2 | Rm1 | hyd | 6 ± 1.4 |
| Order Macroscelidea | | | | | |
| Family Macroscelidae | | | | | |
| *Elephantulus* | AMNH115725 | 1 | Rm1 | prd | 30 |
| *brachyrhynchus* | AMNH115729 | 1 | Rm1 | prd | 22 |
| *Rhynchocyon cirnei* | AMNH 49442 | 3 | Rm1 | prd | 35 ± 5.0 |
| | AMNH 49443 | 3 | Rm1 | prd | 34 ± 3.6 |
| | AMNH 49444 | 3 | Rm1 | prd | 36 ± 4 |

[1]No evidence of prismatic enamel was found in these specimens.

[2]The depth value for one micrograph is missing from the calculation of average depth.

---

Among living primates, the enamel of *Lemur* sp. and *Galagoides demidovii* exhibit primarily arc-shaped prisms (Fig. 7). In most micrographs, pattern 2 and pattern 3 arrangements are equally common. A single micrograph of *Tarsius bancanus* revealed a combination of circular and arc-shaped, pattern 3 prisms.

### Order Scandentia

Enamel microstructure was sampled from three species of the subfamily Tupaiinae. Specimens of *Lyonogale tana* and *Urogale everetti* exhibit large, arc-shaped prisms that are most often organized into a pattern 3 arrangement (Figs. 8 and 9). In contrast, the enamel of *Tupaia glis* consistently exhibits large pattern 1 prisms (Fig. 10).

### Order Chiroptera

Enamel from several micro- and megachiropteran species was sampled. Among microchiropterans, *Rhinopoma hardwickei* (Family Rhinopomatidae), *Taphozous mauritianus* and *Balantiopteryx plicata* (Family Emballonuridae) all have primarily arc-shaped prisms that are most often organized in packing pattern 3 (Fig. 11). Qualitative aspects of enamel prism morphology did not vary perceptibly among the 11 *Taphozous mauritianus* specimens.

Within the megachiropteran family Pteropodidae, enamel was sampled from individuals of *Rousettus amplexicaudatus* and *Pteropus insularis* (subfamily Pteropodinae) (Fig. 12). The enamel of both taxa exhibits arc-shaped prisms. While the overwhelming majority of prisms are arrayed in the pattern 3 packing arrangement, some isolated patches of pattern 2 prisms are evident. In contrast to all other species in this study, no evidence of prismatic structure was seen within the enamel of *Nyctimene albiventor* or *Paranyctimene raptor* (subfamily Nyctimeninae).

**Table 2.** Number of sampled individuals ($N_I$), means (X) and standard errors (SE) of prism diameter and prism area variables (in $\mu$m). The presence of significant variation was assessed using a non-parametric Kruskall-Wallis test.

| Taxon | ($N_I$) | prism diameter (X ± SE) | prism area (X ± SE) |
|---|---|---|---|
| Order Primates | | | |
| Suborder Strepsirhini | | | |
| Family Adapidae | | | |
| *Adapis parisiensis* | 2 | 4.41 ± 0.113 | 15.26 ± 1.725 |
| *Cantius* sp. | 2 | 4.12 ± 0.102 | 11.68 ± 1.290 |
| *Cantius mckennai* | 2 | 3.94 ± 0.093 | 10.42 ± 0.251 |
| *Notharctus* sp. | 3 | 4.65 ± 0.383 | 14.54 ± 0.765 |
| Family Omomyidae | | | |
| *Teilhardina americana* | 2 | 3.31 ± 0.297 | 7.96 ± 2.871 |
| *Tetonius* sp. | 1 | 3.66 | 9.48 |
| *Washakius insignis* | 1 | 3.93 | 10.32 |
| Family Lemuridae | | | |
| *Lemur* sp. | 1 | 4.22 | 11.53 |
| Family Galagidae | | | |
| *Galago demidovii* | 2 | 3.13 ± 0.255 | 7.42 ± 0.665 |
| Suborder *incertae sedis* | | | |
| Family Tarsiidae | | | |
| *Tarsius bancanus* | 1 | 3.25 | 9.94 |
| Order Scandentia | | | |
| Family Tupaiidae | | | |
| *Lyonogale tana* | 3 | 3.64 ± 0.095 | 8.47 ± 0.458 |
| *Tupaia glis* | 3 | 3.19 ± 0.566 | 8.10 ± 2.650 |
| *Urogale everetti* | 3 | 4.21 ± 0.262 | 11.84 ± 1.527 |
| Order Dermoptera | | | |
| Family Cynocephalidae | | | |
| *Cynocephalus variegatus* | 4 | 3.50 ± 0.070 | 8.22 ± 0.217 |
| Order Chiroptera | | | |
| Suborder Microchiroptera | | | |
| Family Emballonuridae | | | |
| *Balantiopteryx plicata* | 4 | 2.93 ± 0.193 | 6.85 ± 0.422 |
| *Taphozous mauritianus* | 11 | 2.95 ± 0.211 | 7.09 ± 1.014 |
| Family Rhinopomatidae | | | |
| *Rhinopoma hardwickei* | 1 | 3.58 | 9.75 |
| Suborder Megachiroptera | | | |
| Family Pteropodidae | | | |
| *Pteropus insularis* | 4 | 3.45 ± 0.214 | 7.60 ± 0.880 |
| *Rousettus amplexicaudatus* | 3 | 3.54 ± 0.089 | 8.53 ± 1.174 |
| Order *incertae sedis* | | | |
| Suborder Plesiadapiformes | | | |
| Family Phenacolemuridae | | | |
| *Ignacius* sp. | 4 | 4.89 ± 0.376 | 15.39 ± 2.617 |
| Family Plesiadapidae | | | |
| *Chiromyoides* sp. | 1 | 4.29 | 13.74 |
| *Nannodectes intermedius* | 1 | 4.46 | 13.97 |
| *Plesiadapis cookei* | 1 | 4.91 | 17.25 |
| *Plesiadapis rex* | 3 | 4.55 ± 0.183 | 13.08 ± 2.704 |
| *Pronothodectes matthewi* | 3 | 4.10 ± 0.258 | 8.80 ± 0.601 |

**Table 2 continued**

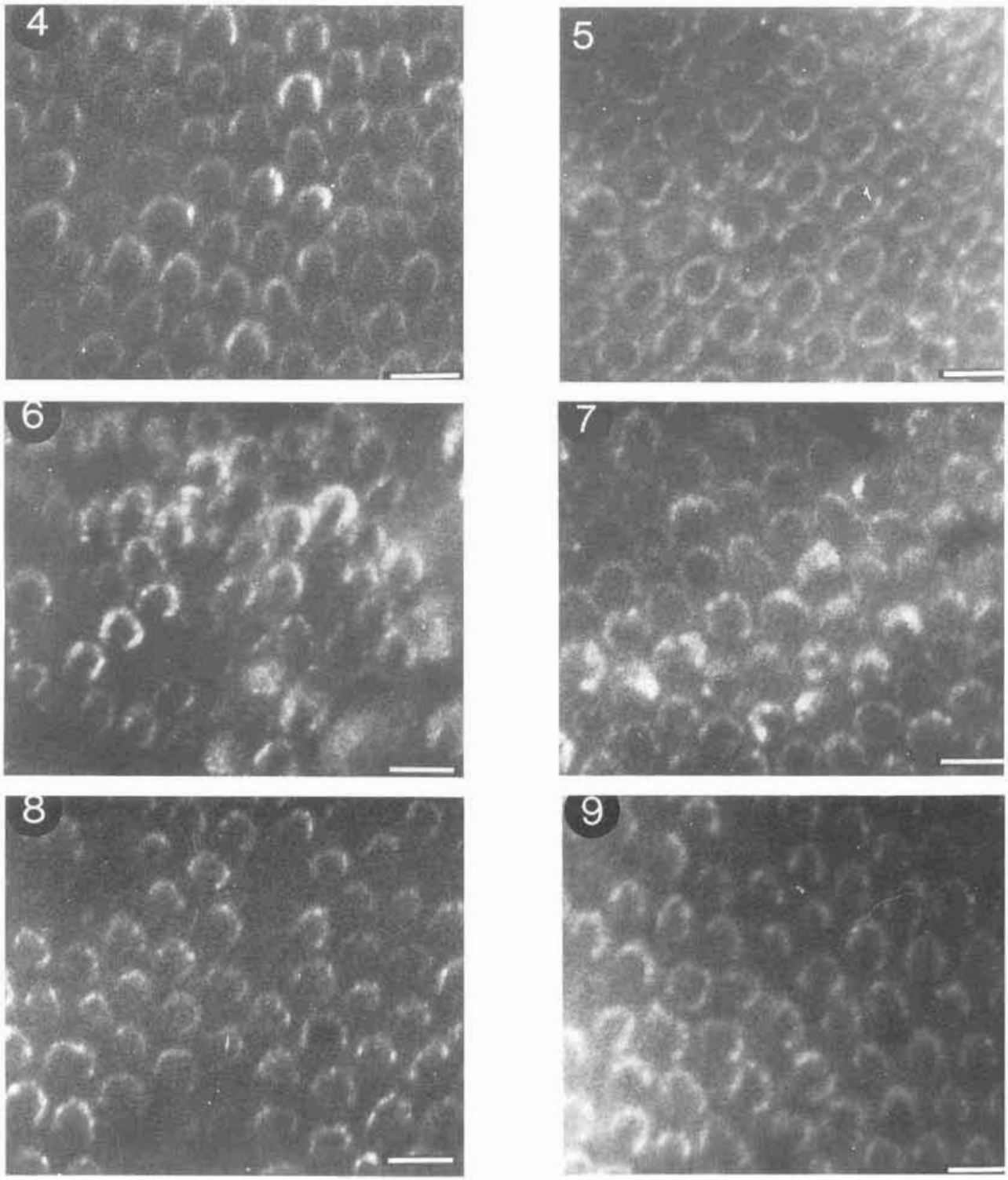
| Taxon | ($N_I$) | prism diameter (X ± SE) | prism area (X ± SE) |
|---|---|---|---|
| Family Microsyopidae | | | |
| *Cynodontomys* sp. | 2 | 3.74 ± 0.559 | 9.57 ± 2.821 |
| *Microsyops* sp. | 2 | 4.63 ± 0.064 | 12.77 ± 1.032 |
| *Niptomomys doreeni* | 2 | 3.47 ± 0.368 | 8.69 ± 2.43 |
| Family Carpolestidae | | | |
| *Carpodaptes hazelae* | 2 | 3.76 ± 0.177 | 9.75 ± 1.351 |
| *Elphidotarsius russelli* | 1 | 3.35 | 7.73 |
| Family Picrodontidae | | | |
| *Picrodus* sp. | 2 | 3.20 ± 0.516 | 8.43 ± 2.694 |
| Family Saxonellidae | | | |
| *Saxonella naylori* | 1 | 3.73 | 9.23 |
| Order *incertae sedis* | | | |
| *Purgatorius* sp. nov. | 2 | 3.47 ± 0.127 | 8.34 ± 0.580 |
| Order Lipotyphla | | | |
| Family Erinaceiidae | | | |
| *Atelerix albiventris* | 3 | 2.49 ± 0.133 | 5.36 ± 0.771 |
| *Erinaceus europaeus* | 5 | 2.56 ± 0.244 | 5.79 ± 1.041 |
| Family Dormaalidae | | | |
| *Litocherus notissimus* | 3 | 2.82 ± 0.399 | 5.50 ± 1.262 |
| Order *incertae sedis* | | | |
| Family Apatemyidae | | | |
| *Apatemys* sp. | 2 | 4.08 ± 0.064 | 9.48 ± 0.870 |
| *Labidolemur kayi* | 1 | 3.39 | 7.63 |
| *Unuchinia asaphae* | 1 | 3.97 | 9.67 |
| Family Leptictidae | | | |
| *Prodiacodon concordiarcensis* | 2 | 3.29 ± 0.431 | 6.71 ± 1.478 |
| Family Mixodectidae | | | |
| *Eudaemonema cuspidata* | 1 | 3.78 | 10.22 |
| *Mixodectes malaris* | 1 | 3.68 | 8.39 |
| Family Nyctitheriidae | | | |
| *Leptacodon tener* | 3 | 2.79 ± 0.254 | 4.98 ± 0.566 |
| *Nyctitherium serotinum* | 1 | 3.00 | 6.57 |
| Family Palaeoryctidae | | | |
| *Palaeoryctes* sp. | 2 | 2.81 ± 0.028 | 5.21 ± 0.318 |
| Family Plagiomenidae | | | |
| *Elpidophorus elegans* | 4 | 5.51 ± 0.453 | 16.00 ± 1.60 |
| *Plagiomene multicuspis* | 2 | 4.33 ± 0.962 | 14.14 ± 3.54 |
| *Planetetherium mirabile* | 1 | 3.98 | 10.44 |
| *Worlandia inusitata* | 2 | 3.84 | 10.49 |
| Order Macroscelidea | | | |
| *Elephantulus brachyrhynchus* | 1 | 3.50 | 8.54 |
| *Rhynchocyon cirnei* | 3 | 3.42 ± 0.448 | 7.85 ± 1.563 |
| Probability that all measurements are drawn from the same population | | $p < 0.0001$ | $p < 0.0001$ |

**Table 3.** Sample sizes (N), means (X) and standard errors (SE) for central distance (CD) and prism area to estimated ameloblast area (PA/AA) variables.

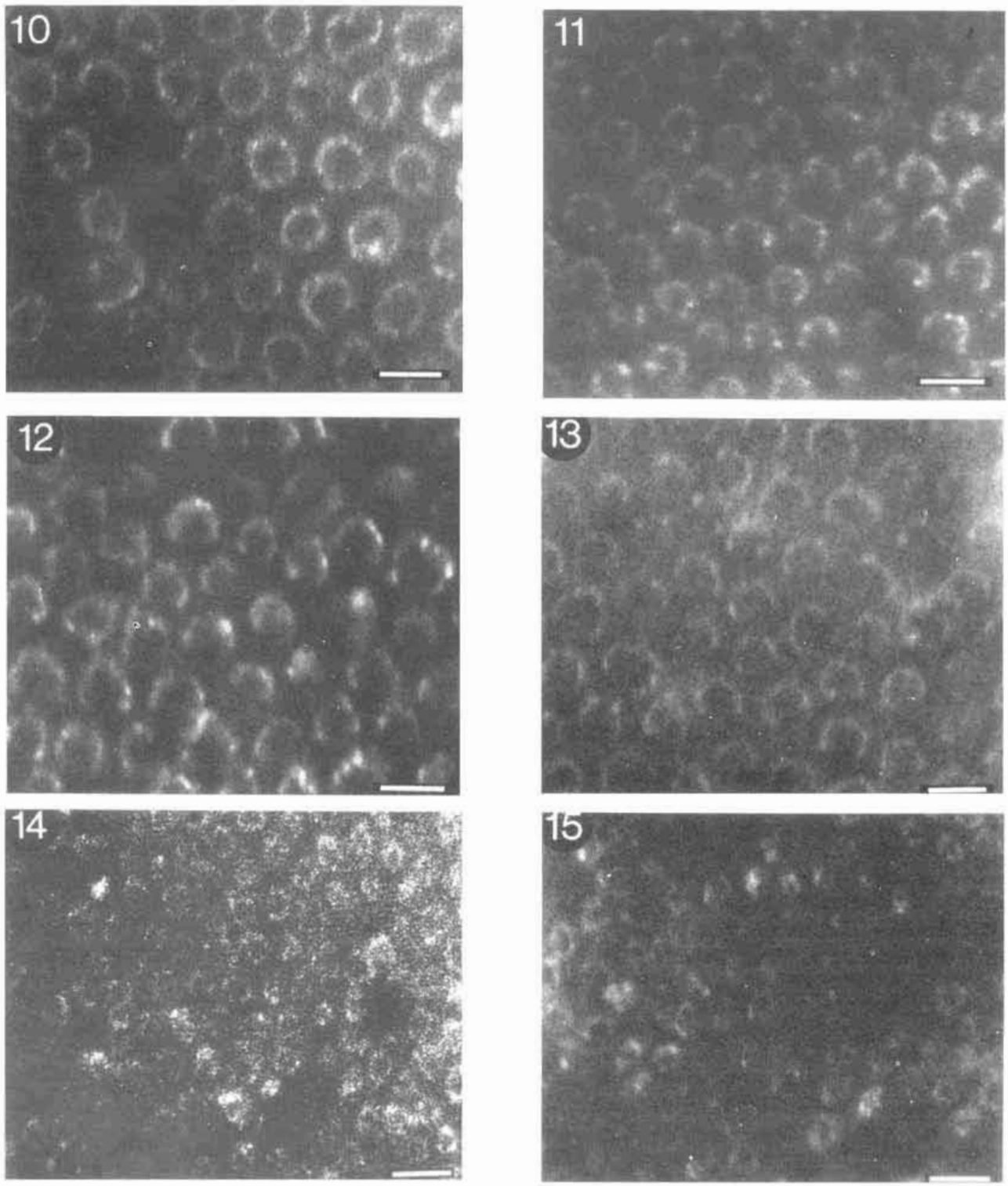
| Taxon | (N) | CD (X ± SE) | (PA/AA) X ± SE |
|---|---|---|---|
| Order Primates | | | |
| Suborder Strepsirhini | | | |
| Family Adapidae | | | |
| *Adapis parisiensis* | 2 | 6.84 ± 0.304 | 0.39 ± 0.006 |
| *Cantius* sp. | 2 | 6.52 ± 0.465 | 0.32 ± 0.012 |
| *Cantius mckennai* | 2 | 6.26 ± 0.058 | 0.31 ± 0.004 |
| *Notharctus* sp. | 3 | 6.50 ± 0.409 | 0.40 ± 0.036 |
| Family Omomyidae | | | |
| *Teilhardina americana* | 2 | 5.66 ± 0.106 | 0.30 ± 0.092 |
| *Tetonius* sp. | 1 | 5.54 | 0.36 |
| *Washakius insignis* | 1 | 6.20 | 0.32 |
| Family Lemuridae | | | |
| *Lemur* sp. | 1 | 6.44 | 0.32 |
| Family Galagidae | | | |
| *Galago demidovii* | 2 | 5.86 ± 0.403 | 0.25 ± 0.011 |
| Suborder *incertae sedis* | | | |
| Family Tarsiidae | | | |
| *Tarsius bancanus* | 1 | 7.01 | 0.23 |
| Order Scandentia | | | |
| Family Tupaiidae | | | |
| *Lyonogale tana* | 3 | 6.30 ± 0.038 | 0.25 ± 0.016 |
| *Tupaia glis* | 3 | 6.17 ± 0.491 | 0.24 ± 0.047 |
| *Urogale everetti* | 3 | 7.04 ± 0.225 | 0.28 ± 0.017 |
| Order Dermoptera | | | |
| Family Cynocephalidae | | | |
| *Cynocephalus variegatus* | 5 | 6.08 ± 0.350 | 0.27 ± 0.048 |
| Order Chiroptera | | | |
| Suborder Microchiroptera | | | |
| Family Emballonuridae | | | |
| *Balantiopteryx plicata* | 4 | 5.09 ± 0.078 | 0.31 ± 0.033 |
| *Taphozous mauritianus* | 11 | 5.70 ± 0.221 | 0.25 ± 0.028 |
| Family Rhinopomatidae | | | |
| *Rhinopoma hardwickei* | 1 | 6.17 | 0.29 |
| Suborder Megachiroptera | | | |
| Family Pteropodidae | | | |
| *Pteropus insularis* | 4 | 6.06 ± 0.358 | 0.24 ± 0.022 |
| *Rousettus amplexicaudatus* | 3 | 5.93 ± 0.049 | 0.29 ± 0.033 |
| Order *incertae sedis* | | | |
| Suborder Plesiadapiformes | | | |
| Family Phenacolemuridae | | | |
| *Ignacius* sp. | 4 | 6.82 ± 0.096 | 0.36 ± 0.052 |
| Family Plesiadapidae | | | |
| *Chiromyoides* sp. | 1 | 6.84 | 0.34 |
| *Nannodectes intermedius* | 1 | 6.84 | 0.35 |
| *Plesiadapis cookei* | 1 | 7.42 | 0.37 |
| *Plesiadapis rex* | 3 | 6.82 ± 0.526 | 0.33 ± 0.054 |
| *Pronothodectes matthewi* | 3 | 6.22 ± 0.39 | 0.25 ± 0.053 |

**Table 3 continued**

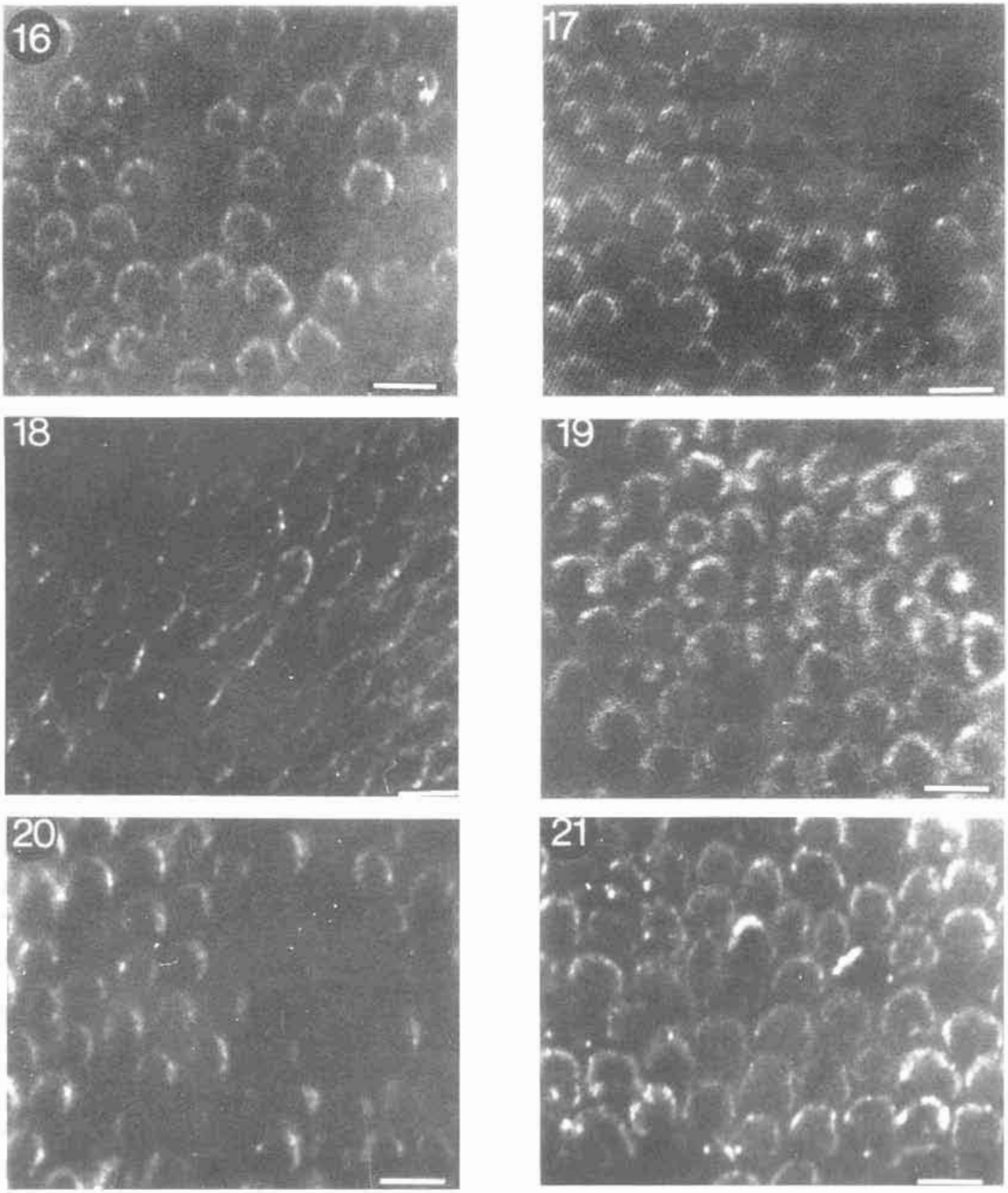
| Taxon | (N) | CD (X ± SE) | (PA/AA) X ± SE |
|---|---|---|---|
| Family Microsyopidae | | | |
| *Cynodontomys* sp. | 2 | 6.70 ± 0.877 | 0.25 ± 0.009 |
| *Microsyops* sp. | 2 | 6.99 ± 0.460 | 0.30 ± 0.017 |
| *Niptomomys doreeni* | 2 | 5.52 ± 0.184 | 0.32 ± 0.024 |
| Family Carpolestidae | | | |
| *Carpodaptes hazelae* | 2 | 6.12 ± 0.064 | 0.30 ± 0.043 |
| *Elphidotarsius russelli* | 1 | 6.07 | 0.24 |
| Family Picrodontidae | | | |
| *Picrodus* sp. | 2 | 5.59 ± 0.580 | 0.31 ± 0.047 |
| Family Saxonellidae | | | |
| *Saxonella naylori* | 1 | 5.89 | 0.30 |
| Family *incertae sedis* | | | |
| *Purgatorius* sp. nov. | 2 | 6.28 ± 0.184 | 0.25 ± 0.005 |
| Order Lipotyphla | | | |
| Family Erinaceiidae | | | |
| *Atelerix albiventris* | 3 | 5.32 ± 0.208 | 0.21 ± 0.026 |
| *Erinaceus europaeus* | 5 | 5.37 ± 0.386 | 0.22 ± 0.029 |
| Family Dormaalidae | | | |
| *Litocherus notissimus* | 3 | 5.64 ± 0.642 | 0.21 ± 0.031 |
| Order *incerta sedis* | | | |
| Family Apatemyidae | | | |
| *Apatemys* sp. | 2 | 6.46 ± 0.177 | 0.26 ± 0.032 |
| *Labidolemur kayi* | 1 | 5.66 | 0.27 |
| *Unuchinia asaphae* | 1 | 6.33 | 0.28 |
| Family Leptictidae | | | |
| *Prodiacodon concordiarcensis* | 2 | 5.95 ± 0.389 | 0.22 ± 0.023 |
| Family Mixodectidae | | | |
| *Eudaemonema cuspidata* | 1 | 6.25 | 0.28 |
| *Mixodectes malaris* | 1 | 5.78 | 0.29 |
| Family Nyctitheriidae | | | |
| *Leptacodon tener* | 3 | 5.00 ± 0.201 | 0.23 ± 0.022 |
| *Nyctitherium serotinum* | 1 | 5.19 | 0.28 |
| Family Palaeoryctidae | | | |
| *Palaeoryctes* sp. | 2 | 5.59 ± 0.255 | 0.19 ± 0.007 |
| Family Plagiomenidae | | | |
| *Elpidophorus elegans* | 4 | 6.70 ± 0.433 | 0.42 ± 0.041 |
| *Plagiomene multicuspis* | 2 | 6.45 ± 0.460 | 0.39 ± 0.043 |
| *Planetetherium mirabile* | 1 | 6.02 | 0.44 |
| *Worlandia inusitata* | 1 | 5.93 | 0.26 |
| Order Macroscelidea | | | |
| *Elephantulus brachyrhynchus* | 1 | 4.81 | 0.39 |
| *Rhynchocyon cirnei* | 3 | 5.82 ± 0.259 | 0.26 ± 0.013 |
| Probability that all measurements are drawn from the same population | | $p < 0.0001$ | $p < 0.0002$ |



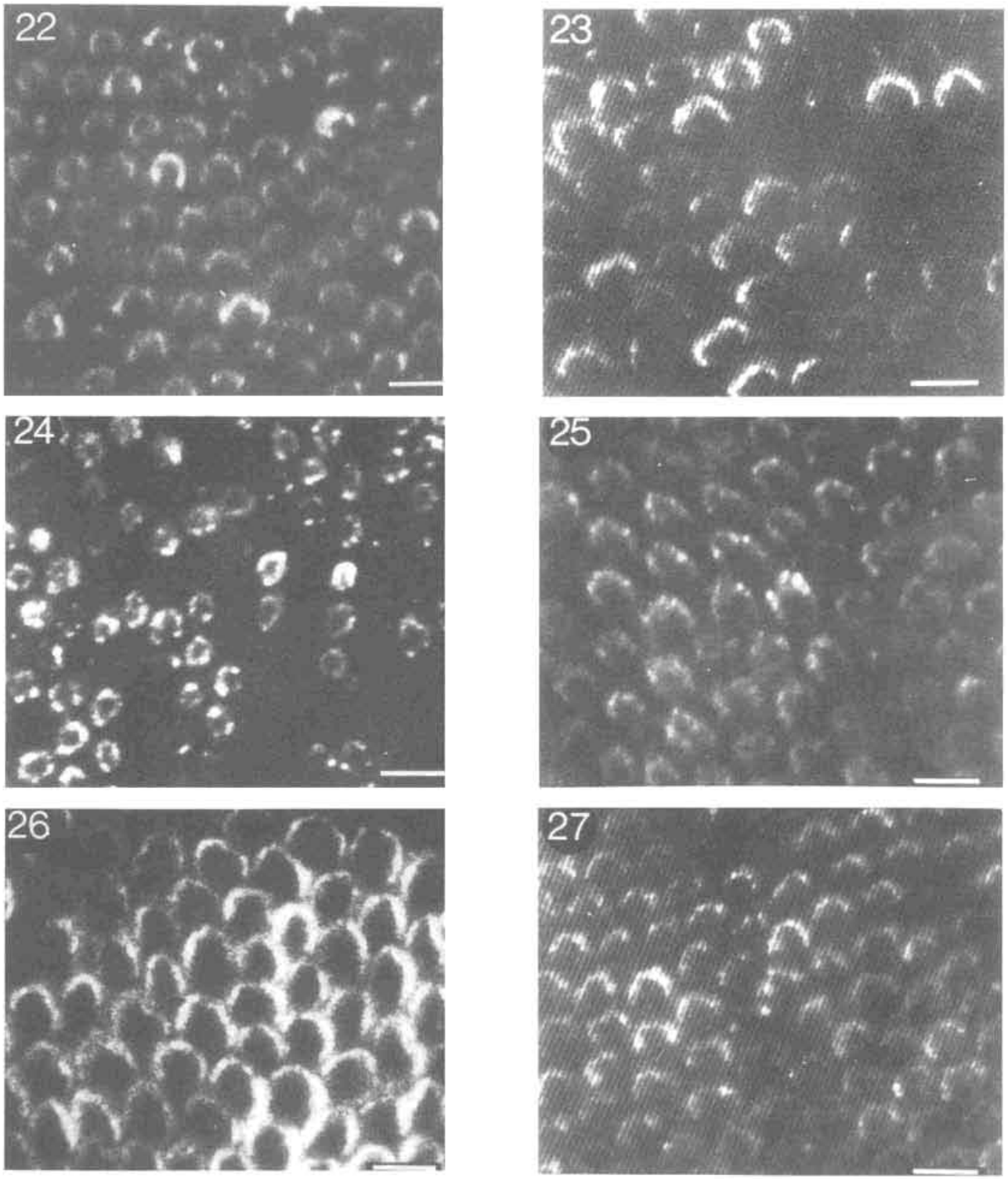

**Figures 4-9.** The enamel of: *Cantius mckennai* (CM 12267) taken at a depth of 30 μm below the buccal surface of the left m1 protoconid (**Fig. 4**); *Adapis parisiensis* (CM 409) taken at a depth of 37 μm below the lingual surface of the left m1 entoconid (**Fig. 5**); *Tetonius* sp. (USGS 5960) taken at a depth of 20 μm below the lingual surface of the right m1 metaconid (**Fig. 6**); *Lemur* sp. (SUSB) taken at a depth of 18 μm below the buccal surface of the left p4 protoconid (**Fig. 7**); *Lyonogale tana* (AMNH 102829) taken at a depth of 40 μm below the buccal surface of the right m1 protoconid (**Fig. 8**); and *Urogale everetti* (AMNH 203290) taken at a depth of 37 μm below the buccal surface of the right m1 protoconid (**Fig. 9**). Bars = 5 μm.



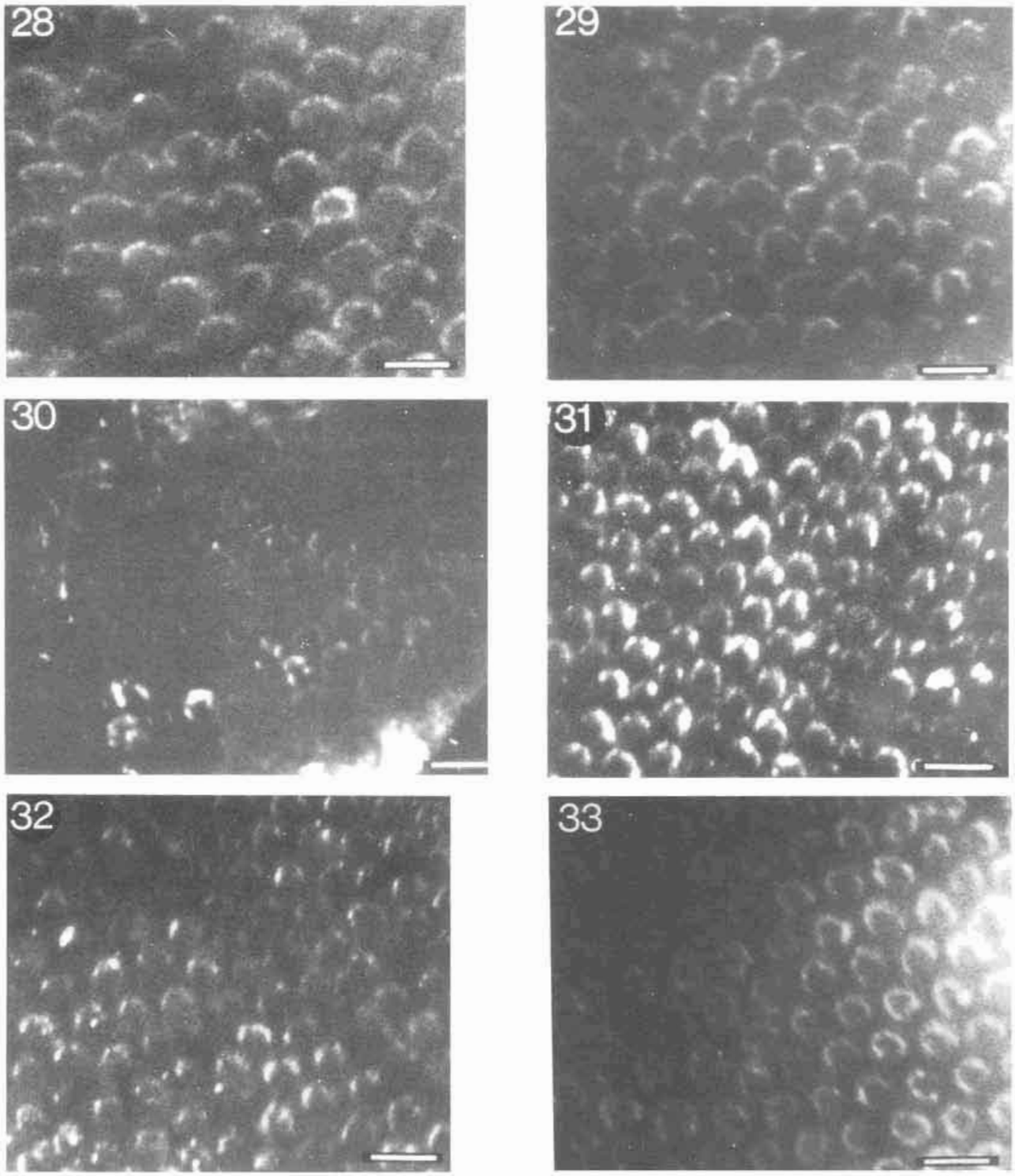

**Figures 10-15.** The enamel of: *Tupaia glis* (SUSB) taken at a depth of 25 $\mu$m below the buccal surface of the right m1 hypoconid (**Fig. 10**); *Rhinopoma hardwickei* (TT 40641) taken at a depth of 16 $\mu$m below the buccal surface of the left m1 hypoconid (**Fig. 11**); *Rousettus amplexicaudatus* (MVZ 141116) taken at a depth of 11 $\mu$m below the buccal surface of the left m1 protoconid (**Fig. 12**); *Cynocephalus variegatus* (RVNH 14516) taken at a depth of 25 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 13**); *Atelerix albiventris* (FSM 20551) taken at a depth of 8 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 14**); and *Erinaceus europaeus* (MVZ 127970) taken at a depth of 20 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 15**). Bars = 5 $\mu$m.




**Figures 16-21.** The enamel of: *Nannodectes intermedius* (UM 83059) taken at a depth of 22 $\mu$m below the buccal surface of the right m2 protoconid (**Fig. 16**); *Plesiadapis rex* (UM 870061) taken at a depth of 18 $\mu$m below the buccal surface of the right m2 protoconid (**Fig. 17**); *Plesiadapis cookei* (UM 63289) taken at a depth of 39 $\mu$m below the right m1/m2 protoconid (**Fig. 18**); *Chiromyoides* sp. (UM 61534) taken at a depth of 30 $\mu$m below the buccal surface of the right m1 or m2 protoconid (**Fig. 19**); *Carpodaptes hazelae* (UM 89943) taken at a depth of 14 $\mu$m below the buccal surface of the left p4 (**Fig. 20**); and *Ignacius frugivorous* (CM 16296) taken at a depth of 25 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 21**). Bars = 5 $\mu$m.




**Figures 22-27.** The enamel of: *Cynodontomys* sp. (CM 41536) taken at a depth of 23 $\mu$m below the buccal surface of the left m1 protoconid (**Fig. 22**); *Microsyops angustidens* (UM 80861) taken at a depth of 40 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 23**); *Picrodus* sp. (UM 19746) taken at a depth of 25 $\mu$m below the buccal surface of the left m1 protoconid (**Fig. 24**); *Purgatorius* sp. nov. (UM 860574) taken at a depth of 10 $\mu$m below the buccal surface of the left m1 protoconid (**Fig. 25**); *Plagiomene multicuspis* (USGS 73034) taken at a depth of 27 $\mu$m below the mesial cingulum of the right m1 or m2 (**Fig. 26**); and *Mixodectes malaris* (AMNH 16604) taken at a depth of 19 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 27**). Bars = 5 $\mu$m.




**Figures 28-33.** The enamel of: *Apatemys* sp. (CM 36257) taken at a depth of 40 $\mu$m below the buccal surface of the right m2 protoconid (**Fig. 28**); *Unuchinia asaphae* (UM 89931) taken at a depth of 34 $\mu$m below the labial surface of the left I2 (**Fig. 29**); *Nyctitherium serotinum* (AMNH 12061) taken at a depth of 19 $\mu$m below the lingual surface of the right m2 (**Fig. 30**); *Leptacodon tener* (UM 89607) taken at a depth of 25 $\mu$m below the buccal surface of the right m1 protoconid (**Fig. 31**); *Prodiacodon concordiarcensis* (UM 84217) taken at a depth of 40 $\mu$m below the buccal surface of a right mx protoconid (**Fig. 32**); and *Palaeoryctes* sp. (UM 84207) taken at a depth of 75 $\mu$m below the lingual surface of the left M1 or M2 protocone (**Fig. 33**). Bars = 5 $\mu$m.

### Order Dermoptera

Enamel was sampled from several specimens of *Cynocephalus variegatus* (Fig. 13). Arc-shaped pattern 3 prisms are by far the most common pattern among the five specimens surveyed here. Occasional circular prisms and small, isolated patches of pattern 2 arrangements are also present.

### Order Lipotyphla

Only small, circular pattern 1 prisms were found within the enamel of the erinaceids *Atelerix albiventris* and *Erinaceus europaeus* (Figs. 14 and 15). In contrast, the enamel of *Litocherus notissimus*, a Paleocene member of the family Dormaalidae, exhibits a combination of small circular and arc-shaped prisms. Although the pattern 3 prism arrangement is predominant among all photomicrographs, significant areas of pattern 2 prisms were also encountered.

### Order Macroscelidea

Enamel was sampled from representatives of each of the two extant macroscelid subfamilies. Mixed pattern 2 and pattern 3 enamel are present among specimens of *Elephantulus brachyrhynchus*. More consistent areas of pattern 3 enamel are present in specimens of *Rhynchocyon cirnei*, although small patches of pattern 2 are also present. Relatively more pattern 2 enamel was found among macroscelideans than in any other sampled taxon.

### Order *incertae sedis*, suborder Plesiadapiformes

Enamel from the plesiadapiform families Plesiadapidae, Carpolestidae, Paromomyidae, Microsyopidae, Saxonellidae and Picrodontidae and the genus *Purgatorius* was sampled. Among the plesiadapids *Pronothodectes matthewi*, *Nannodectes intermedius*, *P. rex*, *P. cookei*, and *Chiromyoides* sp., arc-shaped, pattern 3 prisms are most common although isolated circular prisms are encountered in many micrographs (Figs. 16-19). Arc-shaped prisms also characterize the carpolestids *Elphidotarsius (E.) russelli* and *Carpodaptes (C.) hazelae* (Fig. 20). While *E. russelli* tends to exhibit prism pattern 3, the prisms of *C. hazelae* are often arranged in the pattern 2 configuration.

Like the sampled plesiadapids and carpolestids, the paromomyids *Phenacolemur* sp., *Ignacius frugivorous* and *Ignacius graybullianus* exhibit arc-shaped prisms (Fig. 21). Mixed pattern 2 and pattern 3 prisms characterize both taxa. The microsyopids *Cynodontomys* sp., *Microsyops angustidens*, *M.* sp. indet. and *Niptomomys doreeni* all typically possess arc-shaped, pattern 3 prisms (Figs. 22 and 23). Some circular prisms are evident in micrographs of *Cynodontomys*, while small patches of pattern 2 prisms are found within all microsyopids.

A single genus representing the family Picrodontidae was sampled. While most micrographs of *Picrodus* sp. enamel reveal pattern 3 prisms, the micrograph figured here (Fig. 24) illustrates pattern 1 prisms in a section taken near the outer enamel surface. Finally, like the enamel of most plesiadapiform taxa, *Purgatorius* sp. nov. exhibits arc-shaped, primarily pattern 3 prisms (Fig. 25).

### Order *incertae sedis*, family Plagiomenidae

Enamel was sampled from the traditional plagiomenid genera *Elpidophorus elegans*, *Plagiomene multicuspis*, *Planetetherium mirabile* and *Worlandia inusitata* (Fig. 26). Without exception, arc-shaped prisms characterize the enamel of these taxa; prism pattern 3 was predominant.

### Order *incertae sedis*, family Mixodectidae

The enamel of one individual from each of two mixodectid species was sampled. *Mixodectes malaris* exhibits arc-shaped pattern 3 prisms (Fig. 27). The specimen of *Eudaemonema cuspidata* proved more difficult to image and, as a result, the prism pattern of this specimen is not apparent. Among the five micrographs of this specimen, most prisms are arc-shaped. However, because large areas of prisms could not be displayed, it was not possible to assign *Eudaemonema* to a prism pattern category.

### Order *incertae sedis*, family Apatemyidae

Enamel from each of the apatemyids *Apatemys* sp., *Labidolemur kayi* and *Unuchinia asaphae* exhibit arc-shaped, pattern 3 prisms (Figs. 28 and 29).

### Order *incertae sedis*, family Nyctitheriidae

The several micrographs of a single specimen of *Nyctitherium serotinum* reveal small, arc-shaped, pattern 3 and pattern 2 prisms (Fig. 30). Enamel from individuals of *Leptacodon tener* exhibit very small, arc-shaped prisms (Fig. 31). While most groups of prisms were organized in a pattern 3 configuration, smaller areas of pattern 2 were evident.

### Order *incertae sedis*, family Leptictidae

Enamel from two specimens of *Prodiacodon concordiarcensis* revealed very small, predominantly pattern 3 prisms (Fig. 32).

### Order *incertae sedis*, family Palaeoryctidae

The enamel of *Palaeoryctes* sp. is characterized by a combination of small circular and arc-shaped prisms that are arranged in a pattern 3 configuration (Fig. 33).

## Discussion

Although most of the data presented here describes the enamel structure of species that was previously unknown, some of these results complement previous reports of several species. For example, these confocal

data confirm the presence of circular prisms among lipotyphlous insectivorans and the tree shrew *Tupaia* that were reported in earlier SEM studies (Boyde, 1964; Silness and Gustavsen, 1969; Koenigswald and Clemens, 1992). Similarly, this survey confirms earlier reports that a thick superficial layer of non-prismatic enamel is characteristic of some pteropodid bats (Lester and Hand, 1987).

Primate enamel prism morphology is documented perhaps more extensively than any other mammalian order (with the possible exception of rodents). Not unexpectedly, a great deal of controversy surrounds interpretations of primate enamel morphology. Of the taxa surveyed here, the enamel structure of the genera *Lemur* and *Tarsius* has been surveyed by other workers. Previous investigations of *Lemur* enamel concluded that it is characterized by either pattern 1 (Boyde and Martin, 1982, 1984b, 1987) or pattern 3 prisms (Shellis and Poole, 1977; Shellis, 1984; Maas, 1994). The consistent presence of arc-shaped, primarily pattern 3 prisms within the subsurface enamel of *Lemur* surveyed here supports the latter findings. In contrast, the presence of mixed pattern 1 and 3 prisms within a relatively superficial section through a single specimen of *Tarsius* does little to settle the debate regarding the presence of prism pattern 1, 2 or 3 within the taxon (Grine *et al.*, 1986; Boyde and Martin, 1987).

It seems likely that the solutions to these conflicting interpretations of enamel microstructure will be found through analyses of more exhaustive samples. Many studies have demonstrated that variation in enamel prism morphology occurs at different locations within single teeth as well as among teeth within individual dentitions (Boyde and Martin, 1984b, 1987; Martin, 1985; Stern and Skobe, 1985; Koenigswald, 1992; Koenigswald and Clemens, 1992; Maas, 1993, 1994). Discrepancies between the results presented here and those of previous studies may reflect differences in sampling strategies. It is important to emphasize that the present study is not designed to survey all possible sources of variation in enamel prism morphology. Rather, it is intended to provide a taxonomically diverse data set summarizing a developmentally and functionally homologous location within the dental arcade, i.e., the buccal surface of the lower first molar protoconid. Almost certainly, further surveys of the enamel from the taxa described here that include other tooth positions and functional surfaces will demonstrate variations in enamel microstructural morphology not seen in the present sample.

The most significant aspect of this survey is that it represents a substantial increase in the number of taxa for which enamel prism morphology has been sampled. The enamel microstructure of approximately 75% of the species surveyed here was previously unknown. This large sample provides data from which several important observations can be made.

The most striking characteristic of the enamel sampled in this study is the lack of a clear distinction between prism patterns 2 and 3. Typically, micrographs characterized by arc-shaped prisms contain areas that illustrate cross-sections of both prism types (although the pronounced inter-row sheets characteristic of some pattern 2 arrangements were never present). Similar reports of mixed prism types occurring within the same micrograph are common (Boyde and Martin, 1984b, 1987; von Koenigswald, 1992; von Koenigswald and Clemens, 1992). In this study, species that present arc-shaped prisms in a mixture of pattern 2 and pattern 3 spatial distributions constitute 91% of the sample. Following from the difficulty of assigning arc-shaped prisms to either pattern 2 or pattern 3 categories, it also proved untenable to assign taxa to subcategories of prism packing types (Boyde, 1964; Gantt, 1982, 1983).

An investigation of metrical variation in prism size and spacing does little to subdivide the category "arc-shaped prisms" within this sample. Boyde (1969) demonstrated that pattern 2 prisms and their associated ameloblasts are small, pattern 1 prisms and ameloblasts are intermediate in size, and pattern 3 prisms and ameloblasts are largest. To some extent, the prism size and spacing values of the present sample reflect this pattern. Estimated ameloblast areas for pattern I enamel (24.72 $\mu$m - 33.24 $\mu$m) fall within the lower end of the range of estimated ameloblast area values for arc-shaped prisms (21.73 $\mu$m - 47.80 $\mu$m). The taxon with the smallest estimated ameloblast area values ($\bar{x}$ = 20.06), *Elephantulus brachyrhynchus*, is also the taxon that exhibits the largest proportion of prisms with a pattern 2 spatial distribution. However, these relationships do not hold for measurements of prism size. While prism diameter values for taxa with circular prisms (2.49 $\mu$m - 3.19 $\mu$m) fall within the lower range of the distribution of prism diameter values for arc-shaped prisms (2.79 $\mu$m - 5.51 $\mu$m), prism diameter values for *Elephantulus* are quite high ($\bar{x}$ = 3.5 $\mu$m).

Histograms of prism and ameloblast size were constructed as a means of exploring the potential to divide the arc-shaped prisms surveyed here into discrete categories based on the pattern of metric variation described by Boyde (1969). The histograms for all variables depict a normal distribution of values. There was no evidence of a bimodal distribution, which would have suggested the presence of two size-defined populations of arc-shaped prisms.

In the absence of discrete differences in size, prism pattern categories are idealized representations of naturally occurring cross-sectional prism shapes and spatial distributions. As such, it is not surprising that pure

pattern types are not always found. That such a large taxonomic sample would underscore the continuous variation in prism shape and distribution was predicted by Carlson (1990). Most previous surveys have sampled enamel from fewer individuals and species, perhaps making it easier to assign taxa to a single prism pattern category.

If qualitative assessments of enamel microstructure are to be used in analyses of evolutionary relationships, it is essential to define the mixed pattern 2/3 enamel type. One option is to link taxa with prism types based on the dominant prism pattern found among photomicrographs of each taxon. Using this method, most of the taxa surveyed here would be described as having pattern 3 prisms. The presence of pattern 2 prisms would be ignored as a variant perhaps caused by factors such as prism undulation or decussation. This procedure is not entirely satisfactory, however, as it ignores the inherent variation in the spatial distribution among prisms.

The only common feature of the mixed 2/3 pattern is that the prisms are arc-shaped. Therefore, in the present sample, only the categories "arc-shaped" and "circular" can accurately be used to describe qualitative variation in enamel prism morphology. Because of similar variation, these broad categories have also been used in studies of multituberculate enamel (Carlson and Krause, 1985; Krause and Carlson, 1986, 1987).

Koenigswald and Clemens (1992) and Koenigswald *et al.* (1993) developed a model describing the levels of complexity in mammalian enamel and their significance at different levels of the taxonomic hierarchy. According to this model, variation in prism morphology conveys taxonomically significant information at the ordinal or subordinal level. However, prism shape and spatial distribution data essentially lacks variation across the orders of mammals surveyed here. Arc-shaped prisms are characteristic of at least some members of all of the orders that were investigated. Therefore, for these dentally primitive and relatively thin-enameled mammals, prism shape is not a phylogenetically informative character at the ordinal level.

The issue of polarity is an essential component of any phylogenetic assessment of enamel prism evolution. Because it covers a broad range of species and geologic time, this data set offers insights on the polarity of prism shape and spacing among eutherian mammals. On the basis of either commonality or geologic precedence criteria, arc-shaped prisms appear to represent the primitive condition. The arc-shaped prisms of some of the most ancient groups sampled here (the Dormaalidae, Leptictidae and Palaeoryctidae) are small both absolutely and relative to estimated ameloblast area. This corresponds well with Lester's and Koenigswald's (1989) conclusion based on outgroup criteria that small, widely spaced, arc-shaped prisms were characteristic of the last common ancestor of marsupials and eutherians. Within the context of this study, the overwhelming presence of arc-shaped prisms appears to represent the retention of the primitive eutherian condition. This is perhaps not an unexpected result, as the teeth of the taxa reported here are not highly modified from the primitive tribosphenic morphology.

Despite the widespread presence of apparently primitive prisms within the sample reported here, circular prisms do appear among species within the orders Scandentia (*Tupaia glis*) and Lipotyplha (the erinaceids *Atelerix albiventris* and *Erinaceus europaeus*). Whether this represents a shared derived character or a convergence/parallelism is most appropriately addressed by investigating the evolution of prism shape within each order. Because the species that exhibit circular prisms are either geologically recent (the erinaceids) or derived (*Tupaia*, see Butler, 1980; Luckett, 1980), it seems most likely that the presence of pattern 1 prisms is convergent in these taxa. Similar family-level variation in prism shape has been reported by workers focussing on primates and chiropterans (Boyde and Martin, 1982, 1984b; Lester and Hand, 1987; Lester *et al.*, 1988; Martin *et al.*, 1988). The presence of variation in prism patterns within families suggests that prism shape characters may have phylogenetic significance at lower taxonomic levels in some groups.

Prism cross-sectional pattern does not serve to distinguish among the eutherian mammals studied here. However, this does not necessarily preclude the potential phylogenetic significance of variation in prism size among these taxa. Although all circular prisms are relatively small, arc-shaped prisms cover a wide range of values. There is statistically significant variation between species in prism size and spacing measurements ($p < 0.002$; Tables 2 and 3). While this analysis does not address the biological significance of this variation, the patterns of metric variation deserve further investigation. For example, an investigation of the association between prism size and spacing values and patterns of evolutionary relationship either between species at the family level or among families within orders may generate taxonomically interesting results.

## Summary and Conclusions

Confocal microscopy was used to sample enamel microstructure from 55 species spanning 25 families and at least seven mammalian orders. Sampling was limited (where possible) to the buccal surface of the lower first molar protoconid in an effort to compare developmentally and functionally homologous areas. Qualitative assessments of prism shape and spatial distribution reveal

two distinct prism patterns. Relatively few species (3) exhibit only circular pattern 1 prisms, while the majority of species (50) exhibit arc-shaped prisms that included areas of both pattern 3 and pattern 2. No evidence of prismatic enamel was found in two species of bats.

The results of this study emphasize that prism shape (even when sampled from developmentally and functionally homologous locations) is not an informative phylogenetic character at the ordinal level for these dentally primitive and relatively thin-enameled taxa. It is recommended that further evolutionary analyses of the species surveyed here treat prism shape as a binary character with the states "arc-shaped" and "circular." There is significant variation between species in measurements of prism size and spacing, i.e., prism diameter, prism area, central distance between prisms and the ratio between prism and estimated ameloblast area. More detailed analyses of quantitative variation in enamel prisms may prove useful in documenting evolutionary relationships within or among family-level groups.

## Acknowledgments

I thank curators at the following institutions for the loan of specimens used in this study: American Museum of Natural History, New York, NY; Academy of Natural Sciences, Philadelphia, PA; Carnegie Museum of Natural History, Pittsburgh, PA; Department of Zoology, University of Michigan, Ann Arbor; Florida State Museum, Gainesville; Field Museum of Natural History, Chicago, IL; Museum of Vertebrate Zoology, Berkeley, CA; Yale Peabody Museum, Princeton Collection, New Haven, CT; Rijksmuseum Van Natuurlijke Historie, Leiden, The Netherlands; State University of New York at Stony Brook; Texas Tech University, Lubbock; University of Alberta, Edmonton, Canada; University of Michigan Museum of Paleontology, Ann Arbor; U.S. Geological Survey, Denver, CO. This project was supported by an NSF dissertation improvement grant (BNS 8922966).

## References

Boyde A (1964) The structure and development of mammalian dental enamel. Unpublished Ph.D. thesis, University of London.

Boyde A (1969) Correlation of ameloblast size with enamel prism pattern: Use of scanning electron microscope to make surface measurements. Z Zellerforsch **93**: 583-593.

Boyde A (1978) Development of the structure of the enamel of the incisor teeth in the three classical suborginal groups of the Rodentia. In: Development, Function, and Evolution of Teeth. Butler PM, Joysey KA (eds.). Academic Press, New York. pp. 43-58.

Boyde A, Lester KA (1984) Further SEM studies of marsupial enamel. In: Tooth Enamel. Vol. IV. Fearnhead RW, Suga S (eds.). Elsevier Press, Amsterdam, The Netherlands. pp. 442-446.

Boyde A, Martin LB (1982) Enamel microstructure determination in hominoid and cercopithecoid primates. Anat Embryol **165**: 193-212.

Boyde A, Martin LB (1984a) A non-destructive survey of prism packing patterns in primate enamels. In: Tooth Enamel. Vol. IV. Fearnhead RW, Suga S (eds.). Elsevier Press. pp. 417-426.

Boyde A, Martin LB (1984b) The microstructure of primate dental enamel. In: Food Acquisition and Processing in Primates. Chivers DJ, Wood BA, Bilsborough A (eds.). Plenum Press, New York. pp. 341-367.

Boyde A, Martin LM (1987) Tandem scanning microscopy of primate enamels. Scanning Microsc **1**: 1935-1948.

Butler PM (1941) A theory of the evolution of mammalian molar teeth. Am J Science **239**: 421-450.

Butler PM (1956) The skull of *Ictops* and a classification of the Insectivora. Proc Zool Soc London **126**: 453-481.

Butler PM (1980) The tupaiid dentition. In: Comparative Biology and Evolutionary Relationships of Tree Shrews. Luckett WP (ed.). Plenum Press. pp. 171-204.

Carlson SJ (1990) Vertebrate dental structures. In: Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends. Carter JG (ed.). Van Nostrand Reinhold, New York. pp. 531-556.

Carlson SJ, Krause DW (1985) Enamel ultrastructure of multituberculate mammals: An investigation of variability. Contrib Mus Paleontol Univ Mich **27**: 1-50.

Fosse G (1968a) A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. III. The calculation of prism diameters and the number of prisms per unit area in dental enamel. Acta Odontol Scand **26**: 315-336.

Fosse G (1968b) A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. IV. The number of prisms per unit area on the outer surface of human permanent canines. Acta Odontol Scand **26**: 410-433.

Fosse G (1968c) A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. V. Prism density and pattern on the outer and inner surface of the enamel mantle of canines. Acta Odontol Scand **26**: 501-544.

Fosse G (1968d) A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. The vertical compression of the prism patterns on the outer enamel surface of human permanent teeth. Acta Odontol Scand **26**: 545-572.

Fosse G (1968e) A quantitative analysis of the numerical density and the distributional pattern of prisms and ameloblasts in dental enamel and tooth germs. VIII. The numbers of cross-sectioned ameloblasts and prisms per unit area in tooth germs. Acta Odontol Scand **26**: 573-603.

Fosse G, Eskildsen O, Risnes O, Sloan RE (1978) Prism size in tooth enamel of some Late Cretaceous mammals and its value in multituberculate taxonomy. Zool Scripta **7**: 57-61.

Fosse G, Kielan-Jaworowska Z, Skaale SG (1985) The microstructure of tooth enamel in multituberculate mammals. Paleontology **28**: 435-449.

Gantt DG (1982) Neogene hominoid evolution: A tooth's inside view. In: Teeth: Form, Function, and Evolution. Kurten B (ed.). Columbia University Press, New York. pp. 93-108.

Gantt DG (1983) The enamel of Neogene hominoids: Structural and phyletic implications. In: New Interpretations of Ape and Human Ancestry. Ciochon RL, Corruccini RS (eds.). Plenum Press. pp. 249-298.

Grine FE, Martin LB, Fleagle JG (1986) Enamel structure in platyrrhine primates: What are the implications? Am J Phys Anthropol **69**: 208.

Koenigswald Wv (1992) Tooth enamel of the cave bear (*Ursus spelaeus*) and the relationship between diet and enamel structure. In: Memorial vol. Bjorn Kurten. Forsten A, Fortelius M, Werdelin L (eds.). Annales Zool Fennica (spec issue) **28**: 217-227.

Koenigswald Wv, Clemens WA (1992) Levels of complexity in the microstructure of mammalian enamel and their application to studies of systematics. Scanning Microsc **6**: 195-217.

Koenigswald Wv, Martin T, Pfretzschner HU (1993) Phylogenetic interpretations of enamel structures in mammalian teeth: Possibilities and problems. In: Mammal Phylogeny, Placentals. Szalay FS, Novacek MJ, McKenna MC (eds.). Springer-Verlag, New York. pp. 303-314.

Krause DW, Carlson SJ (1986) The enamel structure of multituberculate mammals: A review. Scanning Microsc **4**: 1591-1607.

Krause DW, Carlson SJ (1987) Prismatic enamel in multituberculate mammals: Tests of homology and polarity. J Mammal **68**: 755-765.

Lester KS, Hand SJ (1987) Chiropteran enamel structure. Scanning Microsc **1**: 421-436.

Lester KS, Koenigswald Wv (1989) Crystallite orientation discontinuities and the evolution of mammalian enamel - or, when is a prism? Scanning Microsc **3**: 645-663.

Lester KS, Boyde A, Gilkeson C, Archer M (1987) Marsupial and monotreme enamel structure. Scanning Microsc **1**: 401-420.

Lester KS, Archer M, Gilkeson GC, Rich T (1988) Enamel of *Yalkaparidon coheni*: Representative of a distinctive order of Tertiary zalambdodont marsupials. Scanning Microsc **2**: 1491-1501.

Luckett WP (1980) The suggested evolutionary relationships and classification of tree shrews. In: Comparative Biology and Evolutionary Relationships of Tree Shrews. Luckett WP (ed.). Plenum Press. pp. 3-34.

Maas MC (1993) Enamel microstructure and molar wear in the greater galago *Otolemur crassicaudatus* (Mammalia, Primates). Am J Phys Anthropol **92**: 217-234.

Maas MC (1994) Enamel microstructure in Lemuridae (Mammalia, Primates): Assessment of variability. Am J Phys Anthropol **95**: 221-241.

Martin LB (1985) Significance of enamel thickness in hominoid evolution. Nature **314**: 260-263.

Martin LB, Boyde A, Grine FE (1988) Enamel structure in Primates: A review of scanning electron microscope studies. Scanning Microsc **2**: 1503-1526.

Sahni A (1979) Enamel ultrastructure of certain North American Cretaceous mammals. Palaeontographica **166**: 37-49.

Shellis RP (1984) Inter-relationships between growth and structure of enamel. In: Tooth Enamel. Vol. IV. Fearnhead RW, Suga S (eds.). Elsevier, Amsterdam. pp. 467-471.

Shellis RP, Poole DFG (1977) The calcified dental tissues of primates. In: Evolutionary Changes to the Primate Skull and Dentition. Lavelle LLB, Shellis RP, Poole DFG (eds.). Charles C. Thomas Co., Springfield, IL. pp. 197-279.

Silness J, Gustavsen F (1969) Structure of the organic matrix of dental enamel in the hedgehog (*Erinaceus europaeus*). Odontol Rev **20** (Suppl 19): 1-41.

Sokal RR, Rohlf FJ (1981) Biometry, the Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, New York. pp. 429-450.

Stern D, Skobe Z (1985) Individual variation in enamel structure of the human mandibular first premolars. Am J Phys Anthropol **68**: 201-213.

Wahlert JH (1968) Variability of rodent incisor enamel as viewed in thin section and the microstructure of enamel in fossil and Recent rodent groups. Breviora **309**: 1-8.

Wahlert JH, Koenigswald Wv (1985) Specialized enamel in incisors of eomyid rodents. Am Mus Novit **2832**: 1-12.

## Discussion with Reviewers

**M.C. Maas:** Some previous studies have discussed depth-related variation in prism morphology and enamel types. Can you comment on depth-related variation for the taxa that you sampled, e.g., was there any consistency in depth, or relative depth of the transition from circular prisms to the deeper layer of arc-shaped prisms?
**Author:** Data summarizing the depth of the transition between circular and arc-shaped prisms was not recorded. However, data regarding the thickness of the superficial non-prismatic enamel are available for 44 individuals (23 species). Results of a regression on rank transformed data demonstrate that the thickness of the non-prismatic layer is not significantly associated with either enamel thickness (measured in the same area of the tooth) or tooth area.

**W.v. Koenigswald:** In *Sus scrofa*, I observed the arc-shaped prisms in the HSB (Hunter-Schreger Bands) become circular at the transition to the outer radial enamel. Increasing amounts of IPM (interprismatic enamel) results in *Sus* (having) much smaller but perfectly rounded prisms. Did you find similar modifications? How far does the IPM effects prism cross section?
**Author:** Within the sample presented here, it is common to see a transition from circular to arc-shaped prisms as deeper portions of the enamel are sampled. Because most of these small, thin-enameled species lack decussation, this transition is not associated with a transition between enamel types. Data were not collected to document changes in prism size that occur with this transition. However, taxa that are characterized by circular prisms (*Atelerix*, *Erinaceus* and *Tupaia*) do exhibit relatively low prism to ameloblast area values ($\bar{x}$ = 0.22; range = 0.21 - 0.24) compared to those that exhibit arc-shaped prisms ($\bar{x}$ = 0.30; range = 0.19 - 0.44).

**D.G. Gantt:** You suggest that prism shape can be used only as a binary character with states "arc-shaped" and "circular." You would agree that this view can be applied to confocal or tandem microscopy studies only, while SEM studies of polished and etched enamel have demonstrated three patterns with several subpatterns?
**Author:** Several studies demonstrate that prism cross-sectional shapes are similar when viewed using either confocal or scanning electron microscopy (Boyde and Martin, 1984b, 1987). Therefore, it seems likely that the same problems of identifying subcategories of prism shape would be encountered in a SEM survey of these taxa. This study does not refute the existence of subcategories of the three classic prism packing patterns. It simply demonstrates that they cannot be used to describe the taxa surveyed here.

**D.G. Gantt:** Have you attempted to correlated prism size and prism packing pattern with tooth size, jaw size and/or body size to determine if a relationship exists?
**Author:** Data summarizing the depth from which prism size and spacing values were gathered are available for 44 individuals (23 species). A regression of rank transformed prism size and spacing values against the relative depth from which sections were obtained demonstrated that these variables are not significantly associated. However, other analyses of this data set demonstrate that prism size and spacing measurements (except prism area to estimated ameloblast area) are significantly associated with both tooth area and enamel thickness (measured using confocal microscopy as the distance from the outer enamel surface to the enamel-dentine junction). As reported previously (Dumont, 1995), prism pattern does not appear to be associated with relative enamel thickness.

**D.G. Gantt:** Two species of bats revealed no evidence of prismatic enamel. Did you conduct an SEM analysis of these specimens to confirm your results? Why do you think these species do not have prismatic enamel?
**Author:** The presence of non-prismatic enamel in the bats *Nyctimene albiventor* or *Paranyctimene raptor* was not confirmed using SEM. However, this result is supported by the report of large proportions of non-prismatic enamel in two closely related bats (*Pteropus scapulatus* and *Dobsonia* sp.) (Lester and Hand, 1987). I am currently working to test several alternative hypotheses regarding the underlying basis of this exaggerated superficial layer of non-prismatic enamel.

## Additional References

Dumont ER (1995) Mammalian enamel prism patterns and enamel deposition rates. Scanning Microsc **9**: 429-442.