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ADULT PHYLLOSTOMID (BAT) ENAMEL BY SCANNING ELECTRON MICROSCOPY  
- WITH A NOTE ON DERMOPTERAN ENAMEL

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Abstract

This study assesses the enamel of five phyllostomids of differing feeding habits; only one example of the microchiropteran super-family Phyllostomoidae having previously been studied by SEM. A dermopteran was also examined to ascertain whether the enamel might reveal insectivore, chiropteran or primate characteristics.

The five phyllostomids were found to display the additional crystallite discontinuity feature (minor boundary plane or seam) which is a major characteristic of all the bats we have so far examined - with the exception of two megachiropterans. The enamel of the four fruit and nectar feeders (*Phyllostomus*, *Carollia*, *Glossophaga* and *Artibeus*) is essentially similar and different to that of the blood feeder (*Desmodus*). The differentiating factor for the two groups is the poor degree of prism development in *Desmodus*; the prisms being restricted to the inner two thirds of the enamel over the cusps or sectorial ridge, and lacking in the greater part of the axial and the sulcular enamel. The poor prism development in the vampire bat raises interesting questions from both an ontological and a phylogenetic point of view.

The dermopteran (*Cynocephalus* sp.) displays horse-shoe shaped prisms with associated minor boundary planes (seams); an appearance entirely similar to those microchiroptera we have examined. This finding could be advanced as evidence for a close phylogenetic relationship between the Dermoptera and Chiroptera as these features are not found to the same extent in insectivores or in primates; the other two orders to which dermopterans are assigned.

The evolutionary significance of the seam feature is being studied further; it is very likely to be of importance in unravelling the history of mammalian enamel.

**KEY WORDS:** Bat enamel, Chiroptera, Dermoptera, Phyllostomid, Vampire bat, enamel ultrastructure, enamel prisms.

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Introduction

A baseline description of bat enamel at electron microscope level has recently been provided by Lester and Hand (1987). For that account, representatives of all five superfamilies of the sub-order Microchiroptera and representatives of the sub-order Megachiroptera were surveyed. However, only one example from the microchiropteran super-family Phyllostomoidea was studied. Because no destructive preparation was permitted of that particular specimen as a condition of loan; examination was necessarily restricted to the intact outer enamel surface and to the irregular and occasional functionally worn surfaces. Consequently, the information available from the specimen (*Artibeus* sp.) was limited and no illustration was published.

Subsequent to that study, the complete skulls of five phyllostomids of differing feeding habits were made available (see Acknowledgements) for an assessment of the possible degree of diversity in their enamel. Permission was given to section one tooth from each genus for SEM examination.

Also following on from the initial investigation, it seemed logical to examine a dermopteran (flying lemur or colugo) in order to ascertain whether the enamel might reveal insectivore, chiropteran or primate characteristics as we presently understand them. There is some controversy over the phylogenetic affiliation of this unusual mammalian order and, given the increasing application of enamel ultrastructure to taxonomic considerations (e.g., recent papers by Boyde and Martin, 1984; Krause, 1986; Lester et al., 1987), SEM assessment of dermopteran enamel (see Acknowledgements) seemed bound to provide some useful information.

Materials and Methods

**Phyllostomoidea**

The phyllostomid material was provided (see Acknowledgements) in the form of dried adult skulls of the following genera.

i) *Phyllostomus hastatus*. A mixed feeder eating fruit and small vertebrates; no data on origin or sex, but known to be found in Honduras, Peru, Trinidad, Tobago, Margarite Island and Bolivia (Walker, 1964; Honacki, et al., 1982). Museum specimen no. 256311.

ii) Carollia perspicillata perspicillata. A soft fruit eater also known to eat insects; from Brazil; male. Museum specimen no. 79582.

iii) Glossophaga soricina soricina. A nectar feeder also known to eat fruit and some insects; from Brazil; male. Museum specimen no. 93901.

iv) Artibeus jamaicensis. A firm fruit eater also known to eat insects; from Puerto Rico; female. Museum specimen no. 39118.

v) Desmodus rotundus murinus. A blood feeder, from Mexico; male. Museum specimen nos. 172331 and 172336.

#### Teeth in situ

A whole dentate mandible of each genus was prepared by gently air-polishing<sup>TM</sup> and lightly etching (1% H<sub>3</sub>PO<sub>4</sub> for 5 secs) the tooth surfaces prior to sputter coating with gold. The mandibles were carefully attached to specimen stubs with plastic conductive carbon cement ("LEIT-C-Plast" Neubauer Chemikalien, Munster, W-Germany) to ensure both sufficient stability for low/medium magnification examination in the microscope and their ultimate return to the Museum's collection.

Intact, damaged and functionally worn surfaces of the in situ teeth were also examined where the field and the operating conditions were favourable.

#### Sectioned teeth

As permitted by the Museum, one tooth of each genus was extracted for destructive examination. The teeth were refluxed in a chloroform/methanol mixture for 6 h prior to embedding in Spurr's resin. The embedded teeth were sectioned for SEM examination by grinding and polishing ("Metaserv" hand grinder and rotary polisher, Metallurgical Services, Betchworth, Surrey, England) with diamond lapping compounds ("Dilap" polishing compounds and cloths, Van Moppes Ltd., Gloucester, England) of particle size down to 0.25 μm. The embedded teeth were approached in a direction parallel to their longitudinal axis in order to maximise the likely area of exposed enamel of the very small specimens. At least three different and progressive levels of section were prepared and examined so as to provide a degree of sampling of the whole tooth. The illustrations provided are representative of the enamel structure found and necessarily include tangential sections of lateral parts of the teeth (away from the mid-line). All sections are however along the longitudinal axis as far as that could be arranged given the small size of the specimens. All finally polished surfaces were etched (1% H<sub>3</sub>PO<sub>4</sub> for 5 secs), dehydrated through ethanol and sputter coated with gold.

All specimens were examined in a JEOL 840 SEM at 15 kV. Stereo-pair images with a tilt angle of 10° were recorded where appropriate.

#### Dermoptera

A dried skull identified only as Cynocephalus was made available for limited examination (see Acknowledgements). Cynocephalus is known by two species only and occurs in Indochina (to Java and Borneo) and the Philippines (Honacki, et al., 1982). Both species feed on fruit, buds, flowers and leaves (Walker, 1964).

Two incisors and a single molar only of Cynocephalus sp. were air-polished<sup>TM</sup>, etched, gold coated and the available tooth surfaces examined in the manner described above for the whole chiropteran mandibles.

## Results

### Phyllostomoidea

For each of the five specimens, satisfactory images were obtained of all or part of the dentate mandible; the intact and worn enamel surfaces of teeth in situ; and of the progressively sectioned, tangential/longitudinal enamel surfaces of individual extracted teeth. It became clear that the enamel of the four fruit and nectar feeders (Phyllostomus, Carollia, Glossophaga and Artibeus) was essentially similar and different from that of the blood feeder (Desmodus). The principal features of the five phyllostomids will be described in turn.

#### i) Phyllostomus hastatus

Teeth in situ. The teeth are the most complex and substantial of the specimens examined (partly due to the circumferential platforming or

### Legends to Figures

p = prism  
s = seam  
t = tubule  
d = dentine  
o = outer enamel surface  
j = enamel-dentine junction

Figs. 1 to 10 are of Phyllostomus hastatus

Fig. 1. The anterior segment of the mandible showing slightly worn premolars, canines and incisors. Bar = 1 mm.

Fig. 2. The lower right second molar, the functional facets of which expose enamel and dentine (see Fig. 3 - arrow locates). Bar = 1 mm.

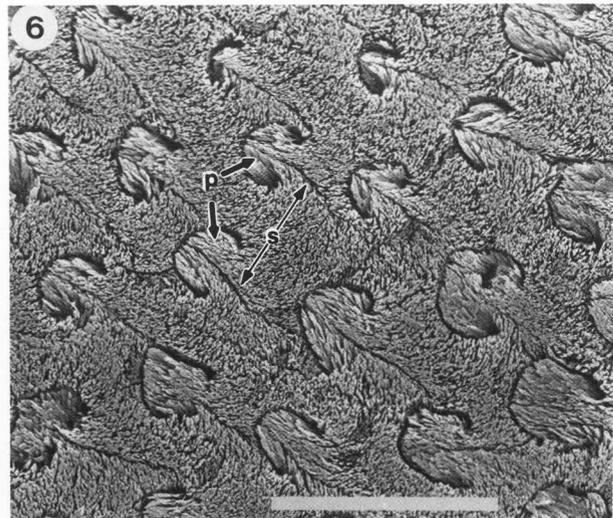
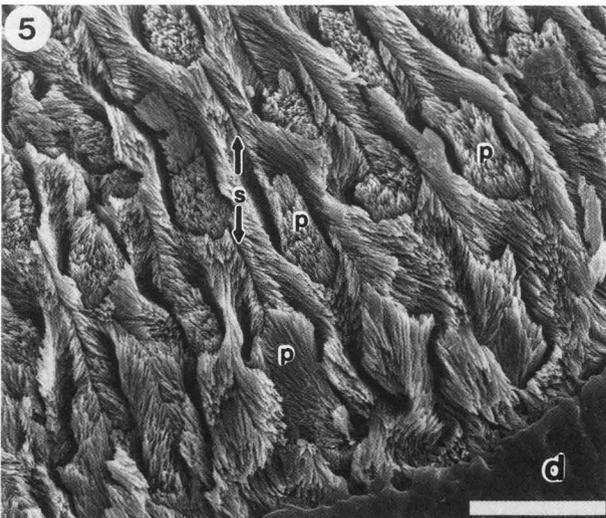
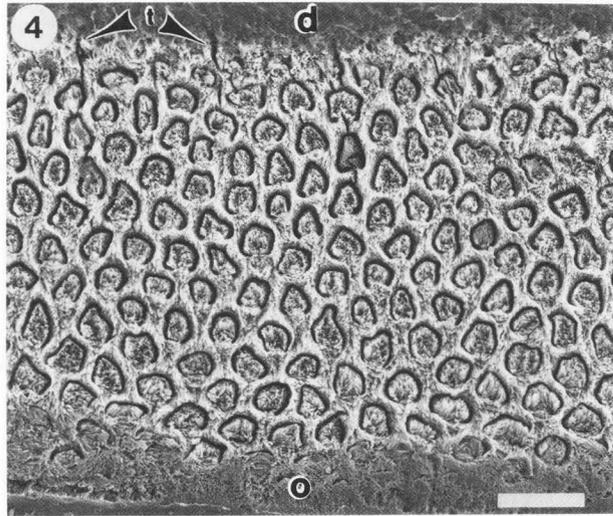
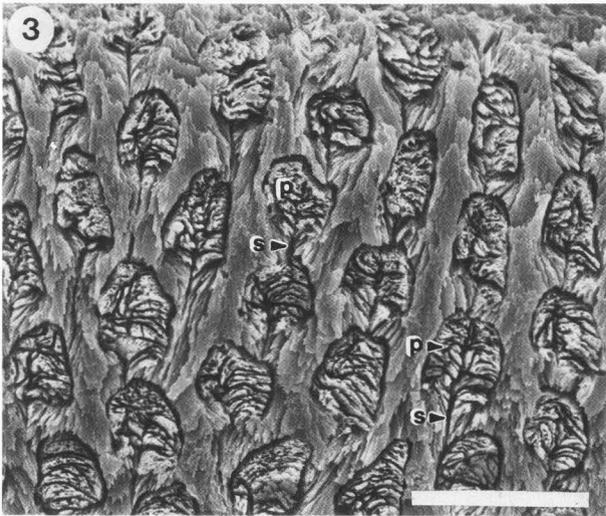
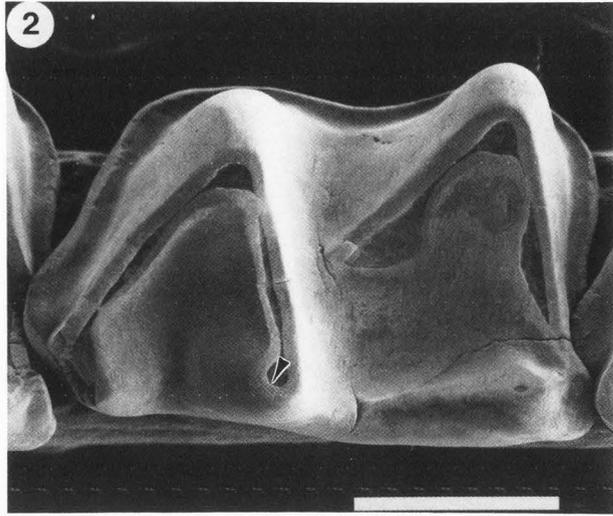
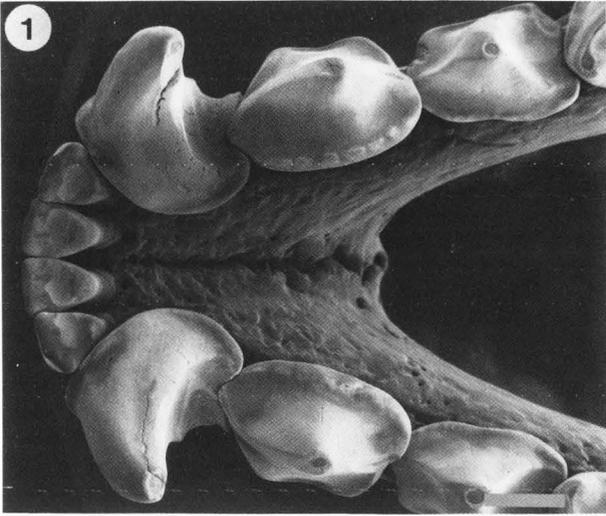
Fig. 3. Functionally worn enamel of the molar illustrated in Fig. 2 - the dentine is to the upper right. Note the open horse-shoe shape of the prisms and the median seams (minor boundary planes) passing into the adjacent inter-prismatic enamel. Bar = 10 μm.

Figs. 4, 5 and 6 are polished, etched sections of enamel from an upper right second molar (section plane parallel to the longitudinal axis of the tooth).

Fig. 4. Full thickness of enamel showing transversely sectioned prisms (dentine to top). Note variation on the basic horse-shoe prism shape and the outer prism free zone (to bottom). There is no completion of prism outline here. Bar = 10 μm.

Fig. 5. Obliquely longitudinally sectioned enamel prisms where the seams (s) run to the specimen surface from beneath the prisms (p) and the rounded (intact) border of the prism horse-shoe is towards the viewer. Bar = 10 μm.

Fig. 6. Obliquely transversely sectioned prisms where the seams (s) are lying on that surface of the prisms (p) towards the viewer and the rounded surface of the horse-shoe lies towards the body of the specimen. Bar = 10 μm.



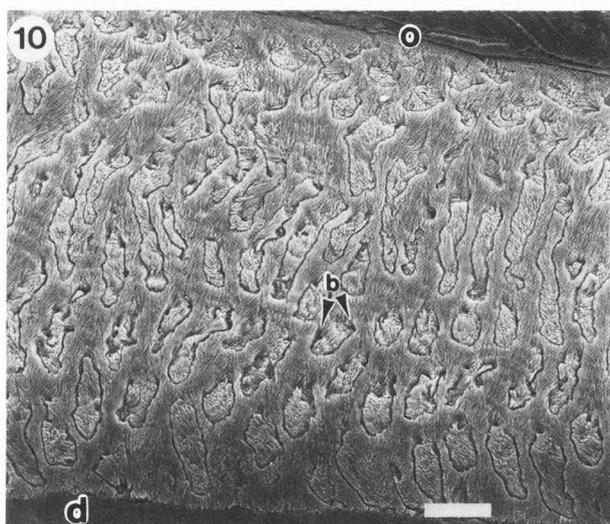
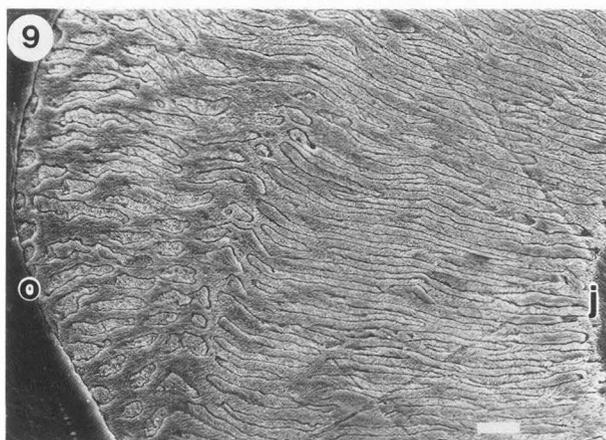
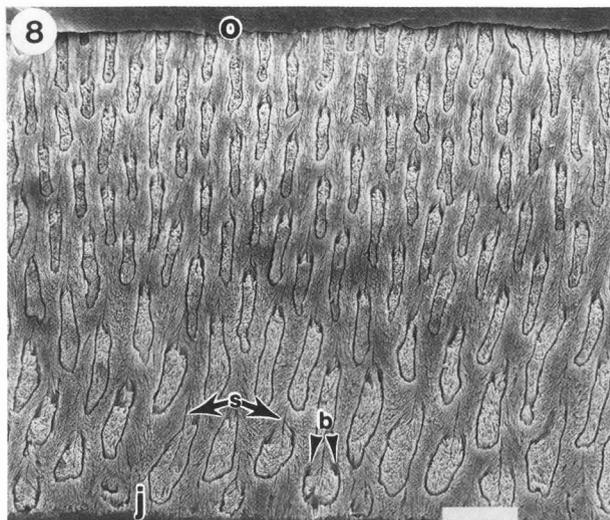
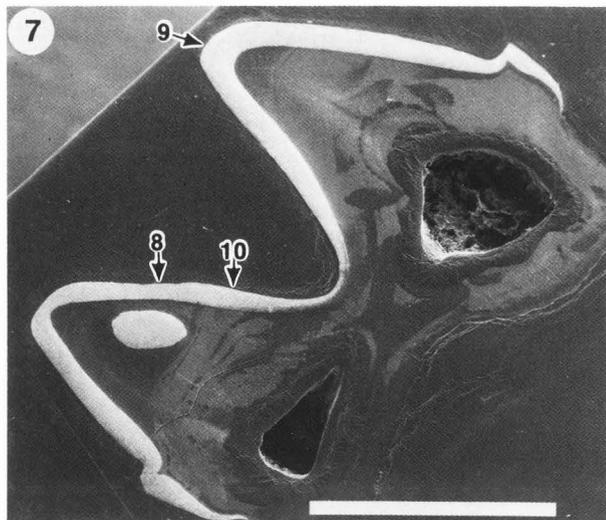


Fig. 7. Longitudinal section of crown of upper right second molar showing relative thinness of enamel and to localize Figs. 8, 9, 10 (see arrows). Enamel island (to lower left) is outer surface in tangential section. Bar = 1 mm.

Fig. 8. Enamel prisms from mid-cuspal slope (see Fig. 7) showing straight parallel prism course. Note the seaming and "bulbs" (b) (see Lester and Hand, 1987) at the open end of the horse-shoe. Note the reduction in the prism diameter and the increase in the number of prisms towards the outer enamel surface - obviously different prism populations from different levels of the crown are represented. Bar = 10  $\mu$ m.

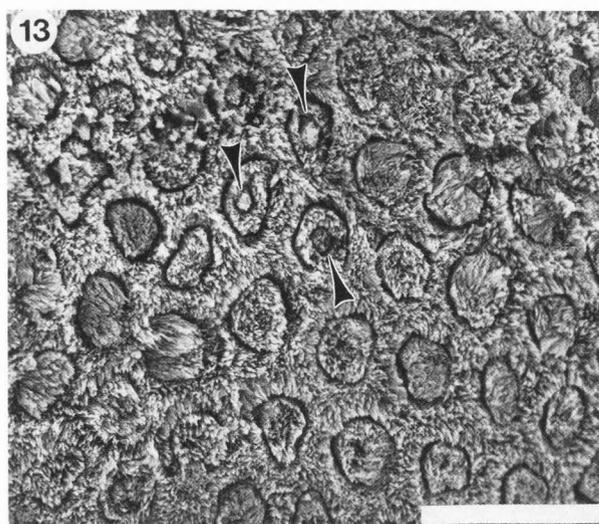
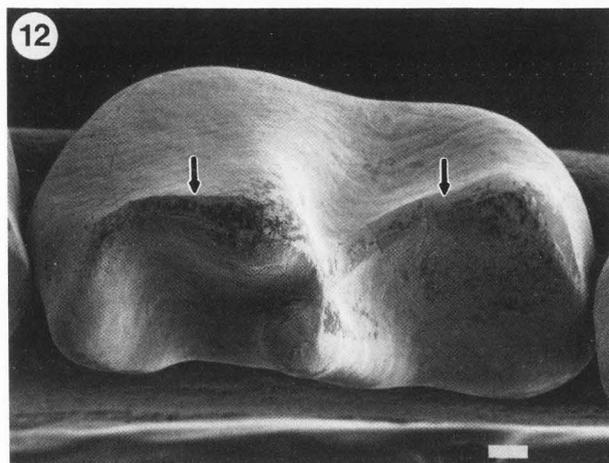
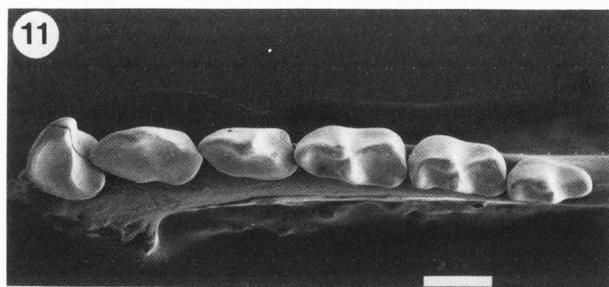
Fig. 9. Cuspal enamel (see Fig. 7) showing the sudden change from straight to undulating prisms in the outer two thirds of the enamel (to left) - the chiropteran equivalent of "gnarled" enamel. Bar = 10  $\mu$ m.

Fig. 10. Enamel towards the sulcular region (see Fig. 7) showing irregular but still parallel course of prisms and exaggerated "bulbs" (b) at the open horse-shoe end of the prisms. Bar = 10  $\mu$ m.

bulbousness of the cervical portions of the canines and posteriors), and the incisors are relatively larger compared to the other mandibular teeth (Figs. 1, 2).

There is considerable wear cuspally in this specimen providing naturally occurring functional sections of the enamel for examination (Fig. 3). These sections reveal the characteristic horse-shoe shape of the enamel prisms and their associated "seams" (additional crystallite discontinuity feature or minor boundary plane). The seams are a major structural feature of bat enamel described in the adult by Lester and Hand (1987) and subsequently related to the developing enamel surface by Lester and Boyde (1987).

Sectioned tooth (upper right second molar). *Phyllostomus hastatus*, having the largest teeth, provided extensive and more easily located fields of enamel in the prepared sections. The prisms are essentially open horse-shoe shaped from the enamel-dentine junction to the prism-free zone (the last-formed 10  $\mu$ m) at the outer enamel surface (Fig. 4). The shape of prisms in



Figs. 11 to 16 are of *Carollia perspicillata perspicillata*

Fig. 11. Lower right mandible. Note reduction of the molar lingual cusps and the relatively minute incisors compared to *Phyllostomus hastatus* (Fig. 1). Bar = 1 mm.

Fig. 12. Lower right second molar showing slight degree of wear over the occlusal ridges (at arrows). Bar = 100  $\mu$ m.

Fig. 13. Detail from one of the worn enamel facets from molar (Fig. 12) showing complete rounded prism outline and "prism-within-a-prism" configuration (at arrows). Bar = 10  $\mu$ m.

transverse section varies from basic, classic horse-shoe to square to ovoid to triangular to spade-shaped. The average maximum transverse diameter of prisms is 2.7  $\mu$ m (range of 1.8 - 4.0  $\mu$ m) and the average secretory territory of an ameloblast here is ca. 20-24 sq.  $\mu$ m. Small tubules cross the enamel-dentine junction and pass for a very short distance into the first-formed enamel.

Figs. 5 and 6 show prisms sectioned in different directions and illustrate the seams from two different perspectives relative to the prism. In the particular area illustrated in Fig. 5, the seam is arriving at the surface of the specimen from beneath the prism and the rounded complete aspect of the horse-shoe shaped prism is towards the viewer and away from the body of the specimen. In another area (Fig. 6), the seam is at the uppermost surface of the prism running in conjunction with the open base of the horse-shoe which is here towards the viewer and away from the body of the specimen. It is particularly clear in this specimen just how profound is the effect of the seams on chiropteran enamel: the seams dominate the substance of the enamel from prism boundary plane to prism boundary plane in the occluso-cervical direction leaving the inter-row sheet (or, more appropriately, inter-prism) with its predominantly, similarly oriented crystallites as the "filler" in-between (Fig. 6).

Variation in prism course according to site is shown in Figs. 7 - 10: an even regular pattern on the mid-cuspal slope (Fig. 8); a mildly convoluted course in the outermost enamel over the cusp (Fig. 9) (? "gnarled enamel"); and a mildly convoluted

course (especially for bats) throughout the enamel thickness (especially towards the sulcular region (Fig. 10). Even in the last instance however, the prisms show no decussation, a parallel prism course being a consistent feature throughout the chiroptera. There is a superficial appearance of tubule development (Fig. 10) but this is more an enlargement of the terminal "bulbs" (see Lester and Hand, 1987) at the ends of the horse-shoe shaped major boundary planes - these would correspond to a complex part of the developing enamel surface in a three dimensional sense which could be expected to leave behind a small void and a correspondingly confused crystallite pattern about it (see Lester and Boyde, 1987).

ii) *Carollia perspicillata perspicillata*

**Teeth in situ.** The teeth are the narrowest bucco-lingually of the four fruit and nectar feeders studied, with the lingual cusp of the molars being very close to the mesio-distal midline (Figs. 11, 12). The very slight wear facets display mostly completed, rounded prisms, some with a "prism-in-a-prism" configuration (Fig. 13). The incisors in this specimen are significantly smaller relative to the other teeth when compared to *Phyllostomus hastatus* (cf. Figs. 1, 11).

Fig. 14. Longitudinal/tangential section of crown (c = cusp) of upper right first molar through a lateral convexity and not including the pulp chamber to localize Figs. 15 and 16 (see arrow). Bar = 100  $\mu\text{m}$ .

Fig. 15. Transversely sectioned prisms showing packing patterns and prism shape.

Fig. 15a. Horse-shoe shaped prisms from mid-third cuspal enamel (see Fig. 14). Bar = 10  $\mu\text{m}$ .

Fig. 15b. Complete prism outlines from outer-third cuspal enamel (see Fig. 14). Bar = 10  $\mu\text{m}$ .

Sectioned tooth (upper right first molar). The bulk of the cuspal enamel is comprised of hexagonally packed horse-shoe prisms unaligned along the longest (occluso-cervical) axis of the horse-shoes in a very ordered pattern typical of marsupial Pattern 2 enamel (see Boyde, 1964; Boyde and Lester, 1967; Lester et al., 1987) (Figs. 14, 15a). The prism outline becomes complete near the outer enamel surface to produce a classical Pattern 1 arrangement (Fig. 15b). Prism course is straight so that the entire length of a prism may be captured in a single section. Where the prisms are obliquely sectioned, seams are evident in contiguity with the open end of the horse-shoe prisms (Fig. 16).

iii) *Glossophaga soricina soricina*

Teeth in situ. The mandible is characterized by three rather than two premolars, all prominently single-cusped and sectorial. From the canine posteriorly, the occlusal surfaces of the teeth (largely unworn) possess well developed dish-like distal triangular elements (Figs. 17, 18). There is not the intimate mesial and distal interdigitation (or overlap) of proximal surfaces as there is for, say, *Phyllostomus hastatus* (cf. Figs. 2, 18). The prism outline is complete at functionally worn surfaces with tubule-like defects appearing both within the prisms and the inter-prism (Fig. 19).

Sectioned teeth (upper left first molar). Examination of the full thickness of enamel confirms the tendency of prisms to complete towards the outer enamel surface (Fig. 20); there is again significant variation in prism shape and diameter. The seams are associated only with the incomplete (horse-shoe) prism outlines.

iv) *Artibeus jamaicensis*

Teeth in situ. The incisors are significantly smaller (not illustrated) and the canines longer and more distally curved compared to the three preceding species (Fig. 21). The molar cusps are small and peripherally placed making the molars appear saucer-shaped in comparison. There is marked wear in this specimen on the second premolar (which displays a worn distal cusp also) and the molars (Fig. 22). There is only faint evidence in isolated areas of prism outlines at the outer enamel surface, the outlines being both complete and incomplete. Where damaged, the enamel shows horse-shoe prisms, seams and a clear prism-free surface zone (Fig. 23).

Sectioned teeth. The prismatic array over the cusps is extremely regular with a transition from horse-shoe to complete where the enamel is

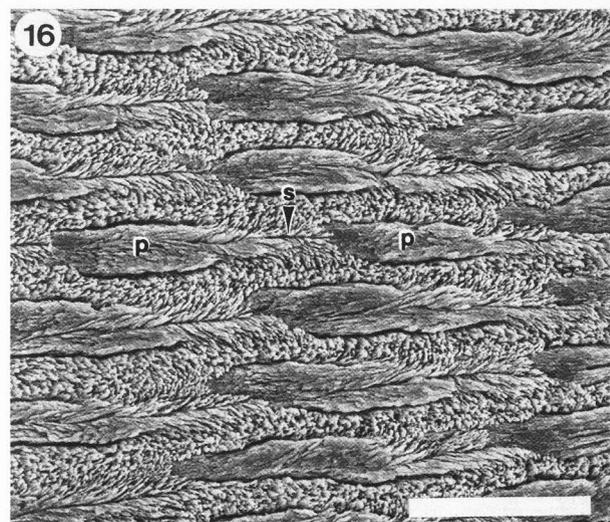
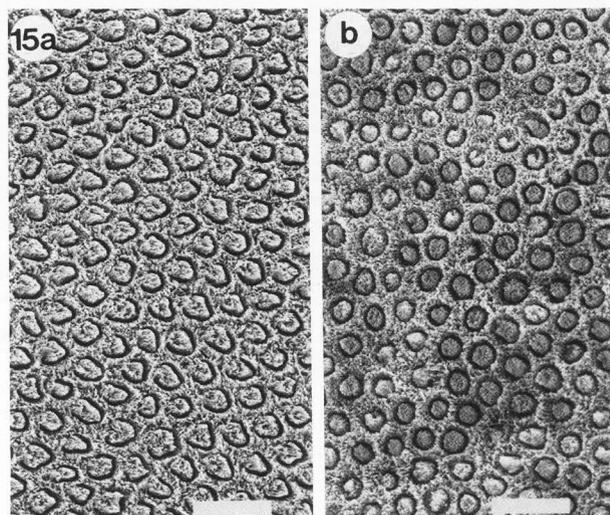
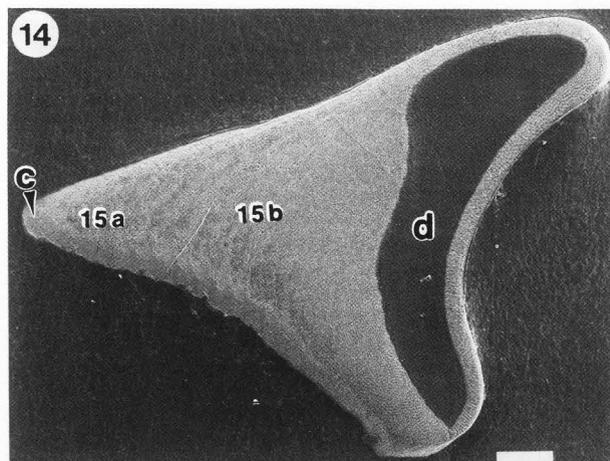
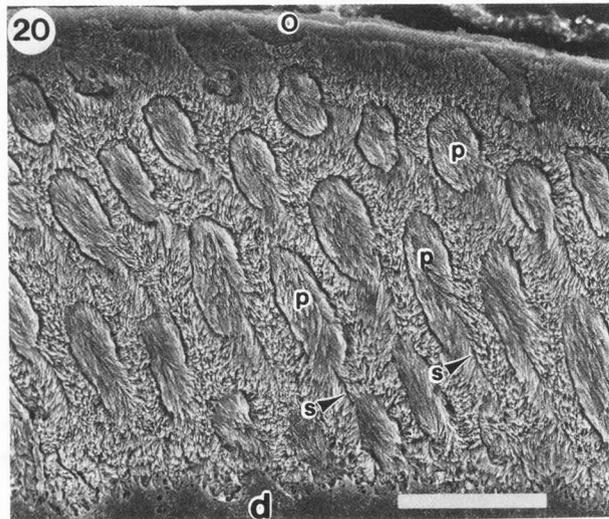
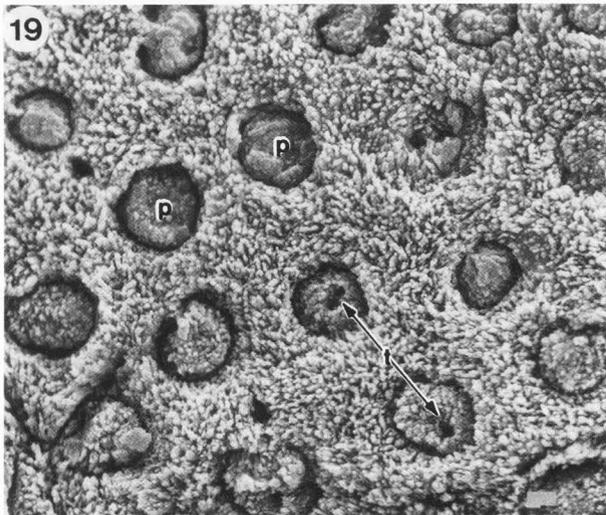
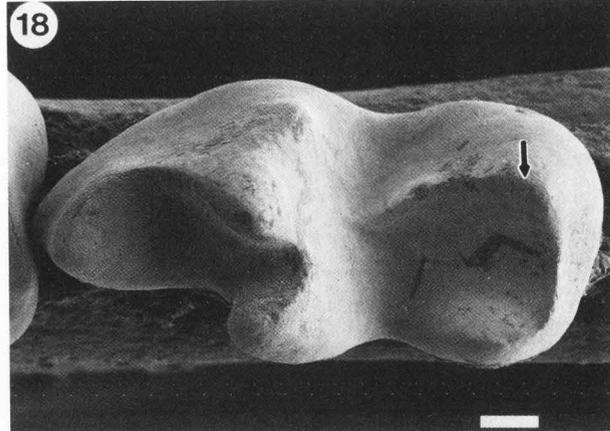
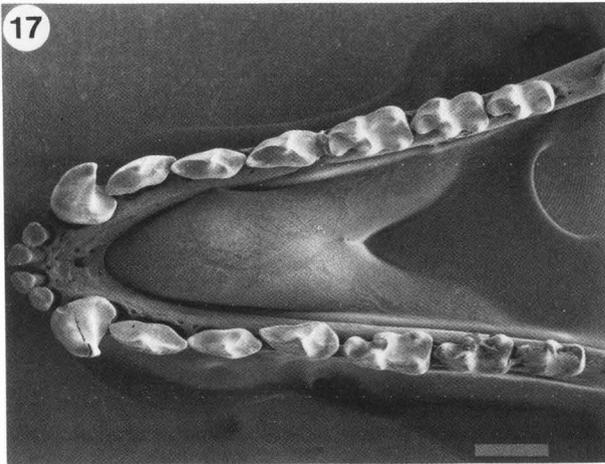


Fig. 16. Oblique longitudinal section of prisms showing extent of seam feature between prisms. Bar = 10  $\mu\text{m}$ .



Figs. 17 to 20 are of *Glossophaga soricina soricina*

Fig. 17. Complete mandible - note the three premolars. Bar = 1 mm.

Fig. 18. Lower right third molar - the proximal surfaces do not interdigitate (arrow locates Fig. 19). Bar = 100  $\mu$ m.

Fig. 19. Enamel exposed on a functional facet of molar shown in Fig. 18. The prism outlines are complete and tubules are present. Bar = 1  $\mu$ m.

Fig. 20. Obliquely sectioned prisms showing the association of seams (at arrows) only with those prisms of open horse-shoe shape (enamel-dentine junction towards bottom). Bar = 10  $\mu$ m.

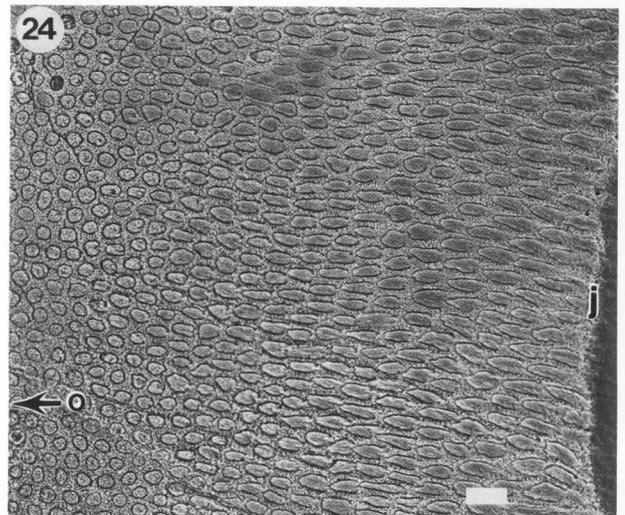
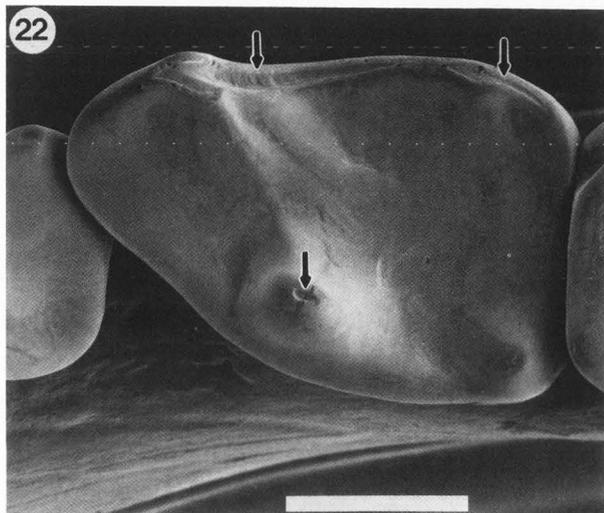
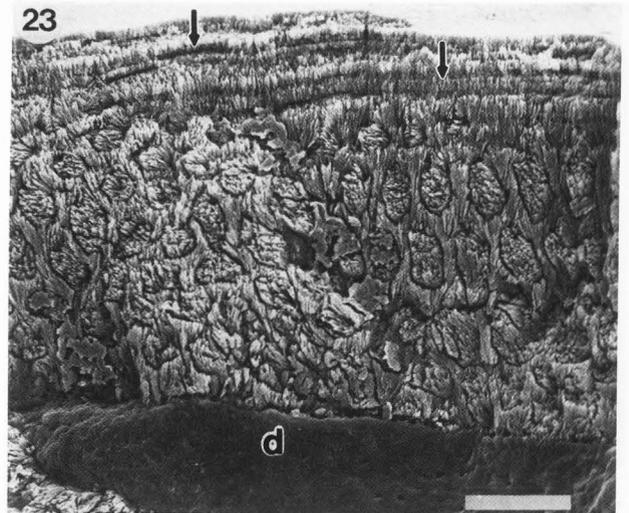
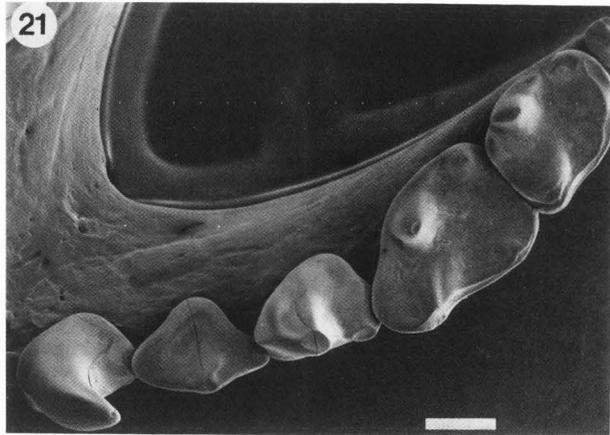
thickest (Fig. 24). In those thinner areas of enamel about the tooth (more especially cervically), the prism outline changes to a less complete arc from the fuller horse-shoe, with a concomitant exaggeration of the seam feature extending radially into a quite marked (slow-forming as judged by the incremental lines) outer prism-free zone (Fig. 25). Some of the prism outlines (major boundary planes) diminish to less than 1  $\mu$ m in length towards the outer enamel surface; this together with the 5  $\mu$ m wide prism-free zone explains the relative lack of clear prism outlines when the outer surface of the tooth is examined.

v) *Desmodus rotundus murinus*

Teeth in situ. All teeth are distinctly buccolingually flattened with a sharp mesio-distal sectorial ridge (Figs. 26, 27). There are only three teeth posterior to the canines which have diastemata on either side; there is another at the mid-line. The incisor crowns have two distinct lobes and cusps. The central premolar is the smallest and constitutes a single cusp to a three-tooth composite sectorial ridge. There is little wear evident and no prism outlines identifiable at all over the intact enamel surfaces. Where the cutting edges are slightly damaged however, there

are suggestions of prism outlines within the substance of the enamel (Fig. 28).

Sectioned tooth (lower right incisor). A longitudinal section displays the bi-cuspid morphology and the extreme thinness of the enamel in the sulcus between the cusps and along the axial surfaces (Fig. 29). Prism outlines are obvious only in the enamel over the cusps and here



Figs. 21 to 25 are of *Artibeus jamaicensis*

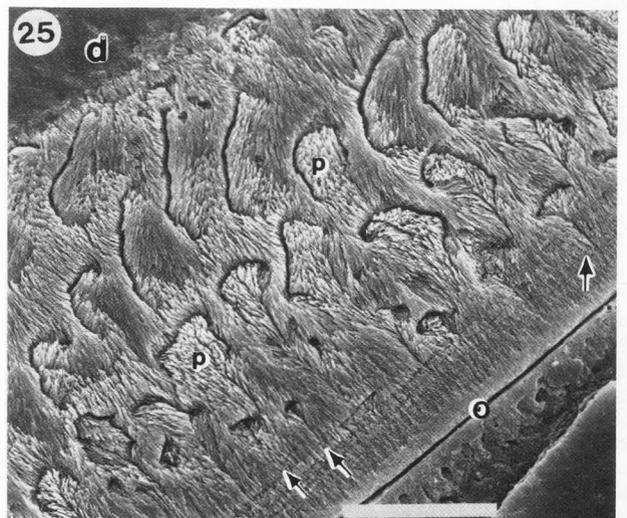
Fig. 21. Lower left mandibular quadrant. Note the distal curvature of canines and the significant bucco-lingual width of molars. Bar = 1 mm.

Fig. 22. Lower left second molar showing functional facetting at arrows (see Fig. 23). Bar = 1 mm.

Fig. 23. Exposed enamel from molar in Fig. 22 showing prism outlines, seaming and incremental lines (at arrows, dentine to bottom). Bar = 10  $\mu$ m.

Fig. 24. Longitudinal section showing transition of prisms from horse-shoe shape at enamel-dentine junction (to right) to complete circles towards outer enamel surface (to left). Bar = 10  $\mu$ m.

Fig. 25. Section shows loss of prism outline towards outer enamel surface (bottom right) but with retention of the seam feature at arrows. Bar = 10  $\mu$ m.



Figs. 26 to 33 are of *Desmodus rotundus murinus*

Fig. 26. Complete lower mandible. Note the extensive diastemata and bi-lobed incisors. Bar = 1 mm.

Fig. 27. The three lower premolars which together constitute an efficient composite sectorial ridge (arrow locates Fig. 28). Bar = 1 mm.

the prism centres are well-spaced and localized to the inner two thirds of the enamel thickness (Fig. 30). Beyond the prismatic enamel, oriented crystallites associated with seams are arranged radially towards the outer enamel surface. This explains the initially puzzling finding that, in longitudinal tangential sections exposing extensive areas of outer enamel, discrete prism outlines were either lacking or indefinite whilst the seams were readily apparent (Fig. 31).

As the enamel thins cervically, prisms become more spaced and less obvious with the seams becoming a dominant feature (Fig. 32). Where the enamel thickness reduces to 10  $\mu\text{m}$  and less, the prisms disappear entirely whilst the seam feature remains (Fig. 33). Further cervically, at approximately 5  $\mu\text{m}$  enamel thickness, the crystallite groups are parallel to each other and thus arranged in neither prisms nor seams.

#### Dermoptera

The dermopteran specimen (*Cynocephalus*) was available on loan for limited surface examination only of previously identified teeth *in situ*.

**Teeth in situ.** The mandibular incisors are unusual in that each takes the form of a blunt seven-pronged fork with the outer prongs providing a scoop-like form (Fig. 34). Where damaged, the enamel can be seen to be prismatic (Fig. 35). The molar is quite extensively worn and cracked (Fig. 36). Facets in the outer enamel surface reveal horse-shoe shaped prisms with associated minor boundary planes constituting the bulk of the enamel (Figs. 37, 38). A prism-free outer enamel zone shows numerous closely spaced incremental lines. The appearance is entirely similar to the same kind of preparation of *Phyllostomus hastatus* and *Artibeus* sp. enamel (cf. Figs. 3, 23 and 37).

#### Discussion

The five phyllostomids surveyed display the additional crystallite discontinuity feature (minor boundary plane or seam) which is a major characteristic of all the bats we have so far examined - with the exception of the megachiropterans *Dobsonia* sp. and *Pteropus* sp. (Lester et al., in preparation). *Dobsonia* sp. has in addition very poor, or hard to demonstrate, prism demarcation overall and, where it is discernible, a fundamentally different prism packing pattern. *Pteropus* sp. has no prism development in the outer third enamel.

The seam feature apart, the five phyllostomids examined fall morphologically and ultra-structurally into two groups with respect to their enamel ultrastructure:

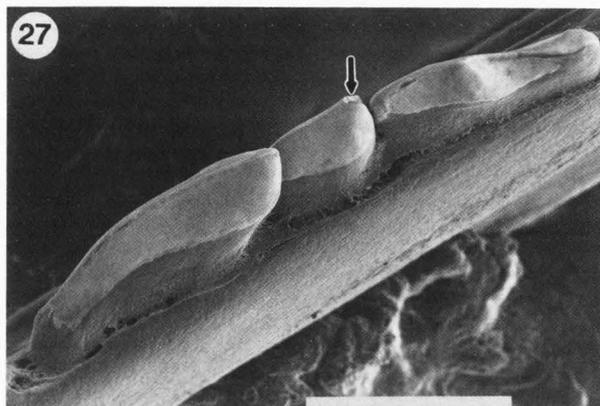
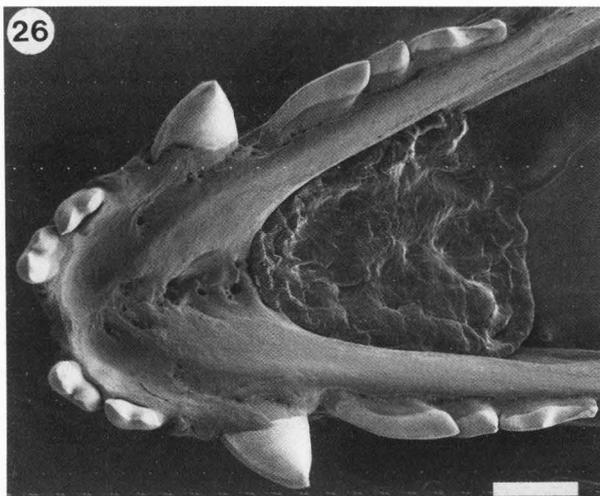
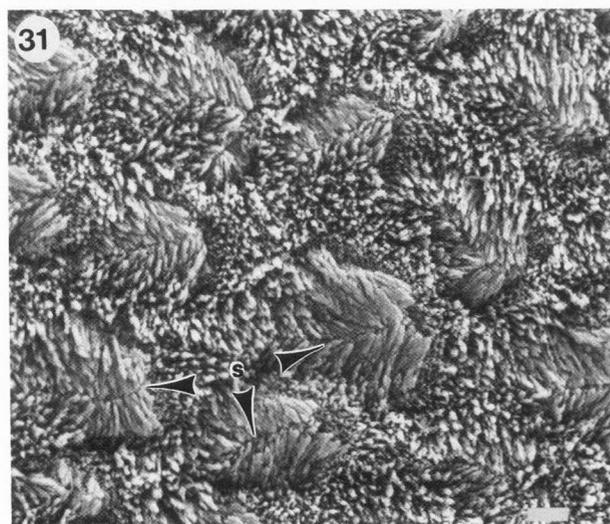
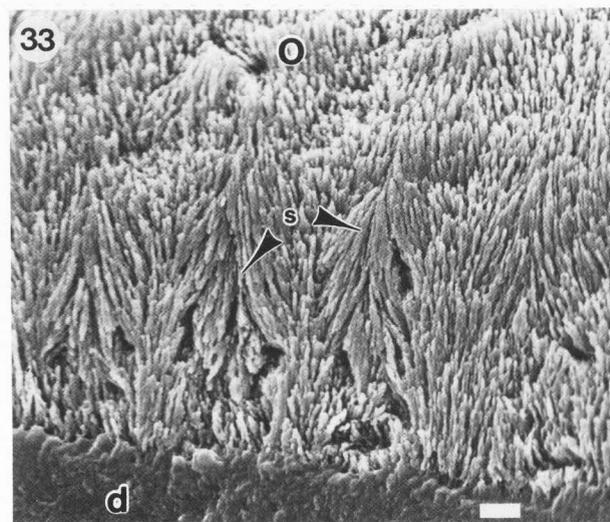
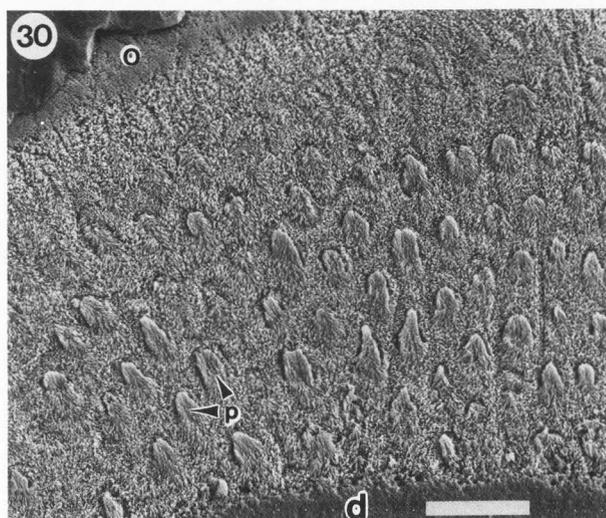
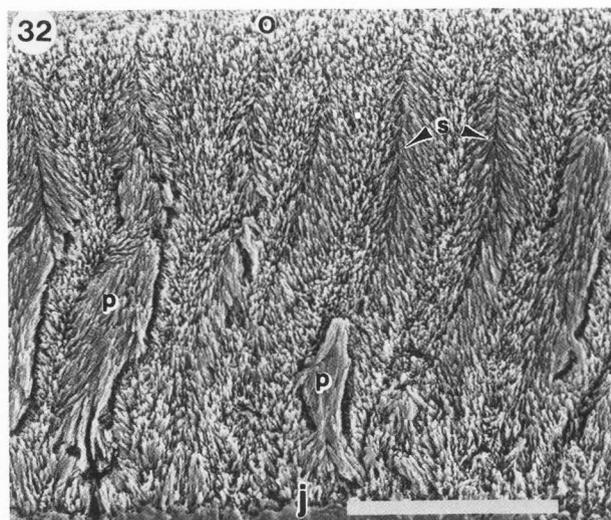
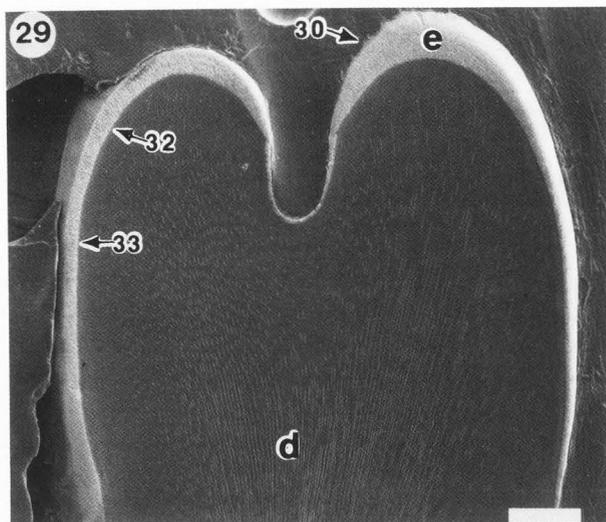


Fig. 28. The damaged portion of the sectorial ridge (see Fig. 27) in which prism outlines may be discerned. The outer enamel surface (at left) drops sharply away and is obviously out of focus at this reduced working distance. Bar = 10  $\mu\text{m}$ .



Figs. 29 to 33 are of embedded, sectioned, lower right incisor.

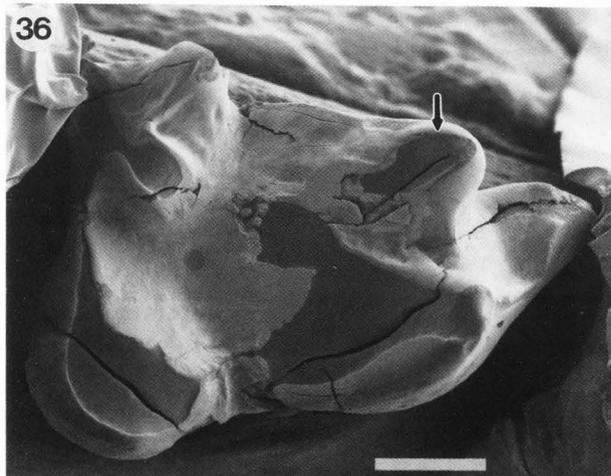
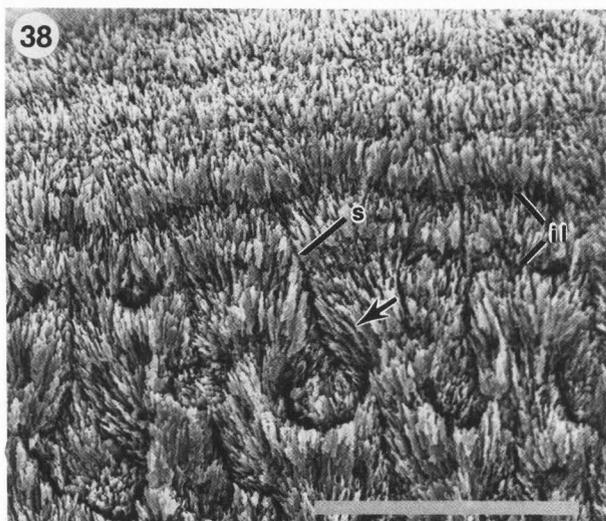
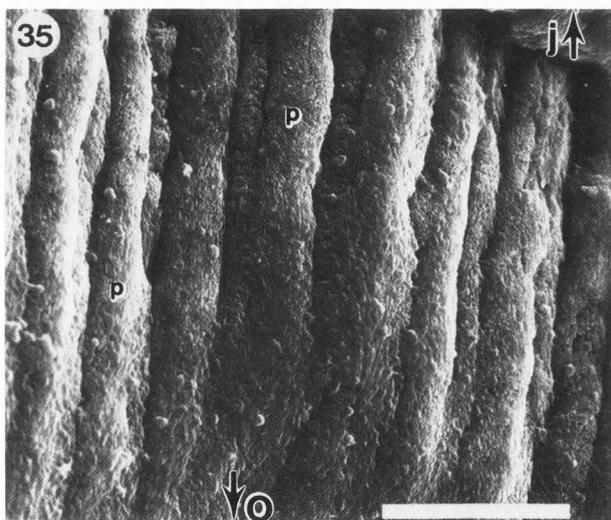
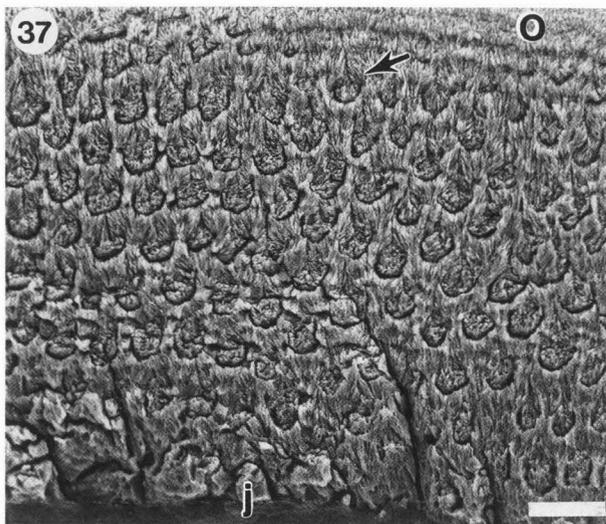
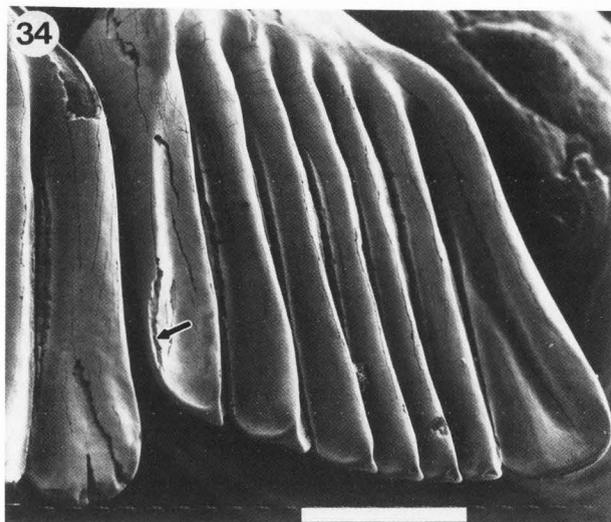
Fig. 29. Longitudinal section for localization of Figs. 30 to 33. Note the extreme thinness of enamel between cusps and axially. Bar = 100  $\mu\text{m}$ .

Fig. 30. Cuspal enamel (see Fig. 29) showing poor prism demarcation restricted to inner two-thirds of the enamel (enamel-dentine junction to bottom). Bar = 10  $\mu\text{m}$ .

Fig. 31. Tangentially sectioned outer enamel showing poor prism demarcation but clear seam formation. Bar = 1  $\mu\text{m}$ .

Fig. 32. Enamel from lateral cusp slope (see Fig. 29) showing gradual loss of prisms but retention of seam feature. Bar = 10  $\mu\text{m}$ .

Fig. 33. Axial enamel (see Fig. 29) showing complete loss of prisms but retention of seam feature. Bar = 1  $\mu\text{m}$ .



Figs. 34 to 38 are of *Cynocephalus* sp.

Fig. 34. Lower right central and lateral incisor. Note the fork-like morphology and slightly damaged enamel coating (arrow locates Fig. 35). Bar = 1 mm.

Fig. 35. Prism demarcation in damaged (fractured) enamel of the central incisor shown in Fig. 34 at arrow. Bar = 10  $\mu$ m.

Fig. 36. Molar of *Cynocephalus* sp. showing extensive wear and cracking artifacts (arrow locates Fig. 37). Bar = 1 mm.

Fig. 37. Full thickness of enamel from functional facet of molar shown in Fig. 36 (enamel-dentine junction to bottom, incremental lines at top). Note the horse-shoe shaped prisms and seams. Arrow locates same feature in Fig. 38. Bar = 10  $\mu$ m.

Fig. 38. High magnification of prism arrowed in Fig. 37 showing detail of crystallite groups about the seam and the incremental lines (il). Bar = 10  $\mu$ m.

- i) the fruit and nectar feeders comprising Phyllostomus hastatus, Carollia perspicillata perspicillata, Glossophaga soricina soricina, and Artibeus jamaicensis; and  
 ii) the blood feeder Desmodus rotundus murinus.

The differentiating factor for the two groups is the poor degree of prism development as a structural feature in Desmodus, the prisms being: well spaced centre to centre; restricted to the inner two thirds of the enamel over the cusps (and/or the sectorial ridge); and lacking in the greater part of the axial and sulcular enamel (cf. Figs. 30, 32, 33).

The poor prism development in Desmodus is very interesting and raises questions from both an ontological and a phylogenetic point of view. Developmentally, it is intriguing that as cuspal enamel gives way to cervical enamel the prisms disappear but the seams survive; indicating perhaps that for this particular enamel the causative groove in the mineralizing enamel front (see Lester and Boyde, 1987) is a more fundamental feature to that surface than the steep walls necessary to produce the major boundary planes demarcating the prism outline. In a sense, this idea is confirmed in Artibeus where, at the outer enamel surface of more cervical enamel, the major boundary plane decreases markedly in extent, as does correspondingly the structural entity or perceived reality of the prism, whilst the seam feature continues to dominate (Fig. 25). At the same time, it is clear that the production of a complete prism outline (requiring a Tomes' process depression at the developing enamel front with a continuous 360° of steep wall to produce the necessary continuous major boundary plane) is exclusive of the developmental groove feature required to produce the seam (or minor boundary plane) so characteristic of bat enamel.

Functionally, the poor prism development observed in the vampire is equally intriguing. To feed successfully, Desmodus must maintain an exceptionally sharp cutting edge on its incisors to open, undetected, shallow wounds in its sleeping prey. Sharpening of the incisors in vampires has been attributed to thegosis; at least in the case of the upper incisors and against horny pads on the tongue rather than of a tooth-to-tooth kind as in rodents for example (Vierhaus, 1983). Non-prismatic enamel may perhaps facilitate the constant maintenance of a razor-sharp edge on these teeth.

From an evolutionary point of view, one could speculate whether with a complete lack of lateral functional masticatory requirement, the vampire bat (Desmodus) - and perhaps at least some megachiropterans - has begun the shift to an early "post-prismatic" enamel phase much as has the platypus (Ornithorhynchus anatinus) (see Lester and Boyde, 1986 and Lester et al., 1987). If this is so, one could predict that an earlier relative of Desmodus would have had a more normal prism pattern and degree of prism development, as was found in the fossil platypus Obdurodon insignis (Lester and Archer, 1986). Vampires are thought to have diverged from other phyllostomids at least 10 million years ago but, as yet, only Pleistocene-aged fossils are known (Hood and Smith, 1982; Hand, 1984).

Poor prism development in the enamel of some members of the Megachiroptera (e.g., the pteropodines Dobsonia sp. (Lester and Hand, 1987) and Pteropus sp. (Lester et al., in preparation)) but not others (e.g., Macroglossus minimus, (Lester and Hand, 1987)) is perhaps more difficult to fathom functionally, but may again be related to diet and also indirectly, size. Except for the large pteropodines (body weight more than 300 g), the fruit- and nectar-eating bats we have examined so far are small bats (of body weight less than 120 g) supplementing their diets opportunistically with insects, or in the case of Phyllostomus small vertebrates, in order to maintain nitrogen requirements. Fruit alone appears to sustain larger megachiropterans as with species of Dobsonia and Pteropus - a diet that may not require a large crushing component in the dentition. Walker (1964) has described feeding behaviour in megachiropterans. Ripe fruit is crushed by the tongue against transverse ridges on the palate and the juice and softer pulp swallowed before the harder pulp and skin is spat out. A diet of fruit alone may perhaps not be too different to one of blood, with little requirement for molars with hard, prismatic outer enamel.

As far as identifying differences amongst the four fruit and nectar feeders examined, there are two features which possibly distinguish Phyllostomus hastatus (a mixed feeder) from the other three: the prisms in Phyllostomus remain horse-shoe shaped throughout the thickness of the enamel (Fig. 4); and the prism course is less regular (straight from enamel-dentine junction to outer enamel surface) as is consistent with the relative complexity of the external morphology of the tooth crowns (Figs. 9, 10).

The ultrastructure of the enamel of the dermopteran Cynocephalus sp., as far as could be glimpsed through surface facets, is quite indistinguishable from bat enamel in general and from Artibeus and Phyllostomus in particular. The finding of the combination of horse-shoe shaped prisms and seams in Cynocephalus could be advanced as evidence for a close phylogenetic relationship between the Dermoptera and Chiroptera (see below). To our knowledge, these features are not found to the same extent in insectivores (Lester, et al., in preparation) or in primates (Boyde and Martin 1982, 1984); the other two orders to which dermopterans are assigned. Shellis (personal communication) has found dermopteran enamel by SEM to be a regular Pattern 2 with Pattern 1 in the outermost enamel.

We are currently searching for the presence or otherwise of the seam feature in a variety of mammalian enamels in order to assess its potential as a taxonomically useful character of enamel (Lester et al., in preparation). It is already clear that, of the extant mammals so far examined, the feature is most marked in the Chiroptera and the Dermoptera. Seams are, however, identifiable to a much lesser degree in certain extant placentals and marsupials in their first-formed enamel. The seam feature also assumes a high level of structural prominence in certain fossil enamels examined (for example, a monotreme and particularly a pacloryctid insectivore).

## Phyllostomid (bat) and dermopteran enamel by SEM.

It is tempting to hypothesize that the presence of the seam feature in a variety of mammalian enamels suggests it to be a symplesiomorphic (or primitive) feature in the Mammalia. Further, its presence only in the first-formed enamel of mammals other than bats and dermopterans suggests that retention of this feature in the adult is a synapomorphic (or shared-derived) character (indicating evolutionary relationship) that would also be found in the common ancestor of the Chiroptera and Dermoptera. A close phylogenetic relationship between these two groups has been proposed by, among others, McKenna (1975). The less attractive, alternative hypothesis with its functional implications is that the unarrested development of this feature has arisen convergently in the two groups, together with horse-shoe shaped prisms.

The evolutionary significance of the seam feature is being studied further, but our impression is that it is very likely to be of importance in unravelling the history of mammalian enamel.

### Acknowledgements

We are extremely grateful to Dr K. Koopman of the American Museum of Natural History, New York for his interest and for kindly making the phyllostomid specimens available. Ms L. Gibson of the Australian Museum was very generous in providing the dermopteran specimen. We wish to thank Ms C. Gilkeson and N. Pigram for their technical assistance and especially Ms J. Longhurst for her unfailing secretarial help.

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### Discussion with Reviewers

**W.G. Young:** Fig. 24 illustrates the transition in prism outline from horse-shoe to complete circles that occurs where the enamel is thickest. Do the prism outlines change in reality or is the graduation in shape in Fig. 24, from circular profiles through horse-shoes to elongate forms, the result of different tangential cuts from transverse to oblique longitudinal section?

**Authors:** Total transverse sections of straight prisms, oblique or otherwise, will distinguish between complete and incomplete prism outlines as is the case in Fig. 24. Predominantly longitudinal sections, however, might not differentiate between the two.

**W.G. Young:** The sectioned tooth from *Desmodus* was a mandibular right incisor and its enamel was thin. The development of the prisms was poor at that site compared with the other genera. Is it possible that a more differentiated enamel might be found on the sectorial blades of the premolars?

**Authors:** As with the other genera, a second tooth (a premolar in this case) was also examined. The prism pattern described is the same for both the incisor and the premolar of *Desmodus*.

**Z. Skobe:** It strikes me that your Figs. 32 and 33 are clear micrographs of what has been described as "pseudoprisms" in mammal-like reptiles (Poole DFG, (1956) *Q. J. Microsc. Sci.* 97, 303-312) but later redrawn to be discredited (Osborn JW, Hillman J, (1979) *Calcif. Tissue Int.* 29, 47-61). Please comment on the possibilities of this implication.

**Authors:** This is a good question but a very complex one. We are not certain that the two papers cited are as opposed in their views as they might seem. As indicated in the Discussion, we currently have in preparation a paper which hopefully will help clarify this question by tracing the evolutionary history of the enamel seams as opposed to focussing on the presence or absence of enamel prisms.