Crystallite Orientation Discontinuities and the Evolution of Mammalian Enamel – Or, When is a Prism?

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CRYSTALLITE ORIENTATION DISCONTINUITIES AND THE EVOLUTION
OF MAMMALIAN ENAMEL - OR, WHEN IS A PRISM?

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Abstract

The nature and relationship of crystallite domains have been explored in fossil and extant enamels spanning an evolutionary period of 200 x 10^6 years. Minor crystallite orientation discontinuities, either linear or planar, were found to be consistent characteristics of all specimens examined.

The earliest minor discontinuity is linear (convergence line), shown here in *Oligokyphus* and *Eozostrodon*. The convergence line would be the result of the occasional development of a conical Tomes' process to the parent ameloblast. An increase in number and regularity of convergence lines, shown here in *Haldanodon*, marks the appearance of a regular pseudoprismatic enamel structure.

The second minor discontinuity to appear is planar (seam), shown here in a dryolestid eupantothere. The seam has previously been deduced to relate developmentally to a central groove on the sloping floor-wall of the Tomes' process pit.

Coincident with the appearance of the seam is that of a rudimentary major planar discontinuity which does not enclose a domain to constitute what would normally be acknowledged as a prism. Its developmental basis would be the establishment of a steep wall and floor (however partial in circumference) to the Tomes' process pit.

The extent of the major planar discontinuities was found to increase subsequently to enclose a classically recognizable prismatic domain, shown here in *Amphiperatherium, Hassianycteris, Smilodon* and *Felis*. This would be consistent with the further development of a definitive floor and wall to the Tomes' process pit.

The sequential appearance of minor linear, minor planar and major planar discontinuities in crystallite orientation is seen as fundamental to the evolution of mammalian enamel structure.

KEY WORDS: enamel, evolution, mammals, prisms, pseudoprisms, convergence lines, seams.

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Introduction

The existence of an additional crystallite orientation discontinuity, minor boundary plane, or seam has been described and illustrated by scanning electron microscopy as a consistent feature of the enamel of many Chiroptera and of the dermopteran *Cynocephalus* (Lester and Hand, 1987; Lester, et al., 1988). The seam occurs where the horse-shoe shaped prism boundary is incomplete and contiguous with the interprism (Fig. 1). Crystallites on either side of the seam lie at an angle to it within the longitudinal axis of the prism so as to subtend an acute angle with the enamel-dentine junction (usually 65-70°). The seams are not evident where the prism boundaries are complete, which, in Chiroptera, is most often in the outer one third where the enamel is thick. The developmental basis for seams has been described in terms of the morphology of the formative front, which, for most practical purposes, may be taken to be the same thing as the mineralizing front. A seam may be related to a consistent groove in the most superficial part of the developing floor wall of the Tomes' process pit (Lester and Boyde, 1987).

A clue to the possible significance of the seam was found in the enamel of the vampire bat (*Desmodus rotundus murinus*) (Lester et al., 1988). Here, the degree of prism development is relatively poor throughout, with normal prism demarcation progressively lost in the outer third of the cuspal enamel and progressively in the thinning cervical enamel. The seams, however, present in conjunction with the prisms, persist in a recognizable form in the absence of definitive prisms both cuspally and cervically (Fig. 2).

We were subsequently impressed by the similarity of these non-prismatic areas of the enamel of *Desmodus* to the enamel of some fossil mammals we had begun to examine. Our aim in this paper is to demonstrate the presence, and discuss the possible evolutionary significance of, both minor and major crystallite orientation discontinuities in the enamel of a range of fossil and extant mammals and in an advanced therapsid. The description of these features, together with a recent analysis of *Procerberus* enamel which displays prismatic, pseudoprismatic and aprismatic forms in the one surface (Lester, 1989b), prompt a fresh look at our conceptualization of the development and evolution of enamel.

A scheme of descriptive terms, with suggested preferred terminology *in italics* and alternative terms (in brackets), is offered below together with some definitions.

Crystallite orientation in enamel may be:
. continuous - *aprismatic enamel* (non-prismatic, prismless)

or

. <u>discontinuous</u> - *pseudoprismatic enamel*[#] (pre-prismatic); *prismatic enamel*

   if discontinuous, the discontinuity may be:
   . linear - *convergence line*[*]
     or
   . <u>planar</u>
      if planar, the discontinuity may be:

Geological

    . minor - *seam*[+] (minor boundary plane)
     or

time

    . <u>major</u>[ø]
      if major, the discontinuity may be:
      . rudimentary
      . partial - *partial prism boundary*
      . definitive - *prism boundary* (major boundary plane, border discontinuity, prism sheath, prism border)

<u>Definitions</u>

[#] <u>Pseudoprismatic enamel</u>: is a discontinuous enamel characterised by repetitive domains related developmentally to conical Tomes' processes. Each domain (pseudoprism) is organised between minor linear discontinuities in crystallite orientation (convergence lines) each of which traces the path of the tip of the Tomes' process of the parent ameloblast through the enamel during formation.

[*] <u>Convergence line</u>: is a minor linear discontinuity in crystallite orientation and appears as a convergence of crystallite tips on a linear focus. It is related developmentally to and traces the withdrawal of the conical tip of the Tomes' process of the ameloblast through enamel during development.

[+] <u>Seam</u>: is a minor planar discontinuity in crystallite orientation and appears as a convergence of crystallites to form a minor boundary plane often in association with a typical horseshoe-shaped prism. It is related developmentally to the occurrence of a central groove on the more superficial part of the sloping floor-wall of the Tomes' process pit.

[ø] A <u>major planar discontinuity</u> in crystallite orientation is a plane in enamel at which crystallite orientation changes suddenly between adjacent domains. Developmentally, it is related to a sharp change in orientation of the surface of the developing front of enamel, usually surface concavities and usually only within the Tomes' process pits. These discontinuities are the prism borders and are the sites where the prism sheath will develop during enamel maturation (adapted from Boyde, 1964; 1967; 1976).

A <u>domain</u> is a volume of enamel in which the crystallite orientation changes only gradually or not at all and the borders are formed by crystallite orientation discontinuities. Developmentally, a domain is related to a flat or gently curved (usually convex) developing front of enamel (adapted from Boyde, 1964; 1967; 1976).

Fig. 1. *Syconycteris australis* (chiropteran) enamel: oblique transverse section of prisms in a polished, etched specimen showing the consistency and regularity of the seams (at arrows) in association with the open ends of the horseshoe-shaped prisms (p) and contiguous interprismatic enamel (ip). Bar = 10 μm.

Fig. 2. *Desmodus rotundus murinus* (chiropteran) enamel: longitudinal section of outer third of cuspal enamel in a polished, etched specimen showing the persistence of a seam (? convergence line) (arrowed) in the absence of a definitive prism. Bar = 1 μm.

Fig. 3. *Oligokyphus* sp. (ictidosaurian therapsid) enamel: etched transverse fracture in cervical region showing convergence lines (at arrows), with associated angled crystallites, extending through the bulk of the enamel thickness (edj - enamel-dentine junction; oes - outer enamel surface). Compare with Fig. 2. Bar = 10 μm.

Fig. 4. *Eozostrodon parvus* (morganucodontid mammal) enamel: etched transverse fracture in cuspal region showing convergence lines (at arrows), with associated angled crystallites, extending through total enamel thickness (edj - enamel-dentine junction; oes - outer enamel surface). Bar = 1 μm.

Fig. 5. *Eozostrodon parvus* (morganucodontid mammal) enamel: etched, longitudinal fracture of occlusal region showing four vertical pseudoprismatic elements extending from enamel-dentine junction (edj) to outer enamel surface (oes). Bar = 1 μm.

Fig. 6. *Haldanodon expectatus* (docodont mammal) enamel: etched, longitudinal fracture of cuspal region showing detail of orientation of crystallite groups forming pseudoprisms about regularly recurring convergence lines (at arrows) (edj - enamel-dentine junction). Bar = 10 μm.
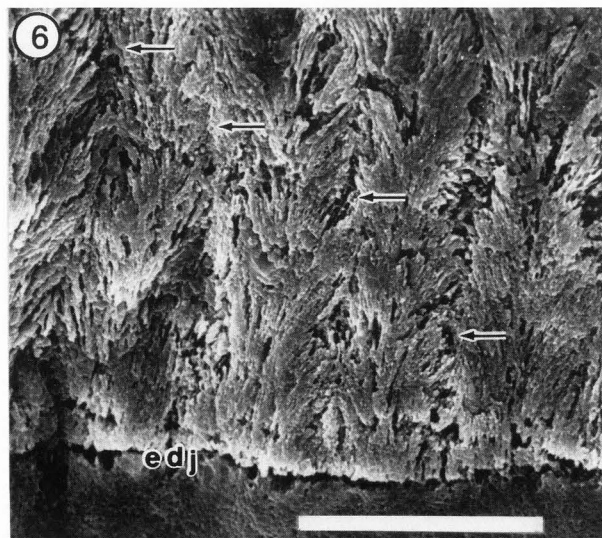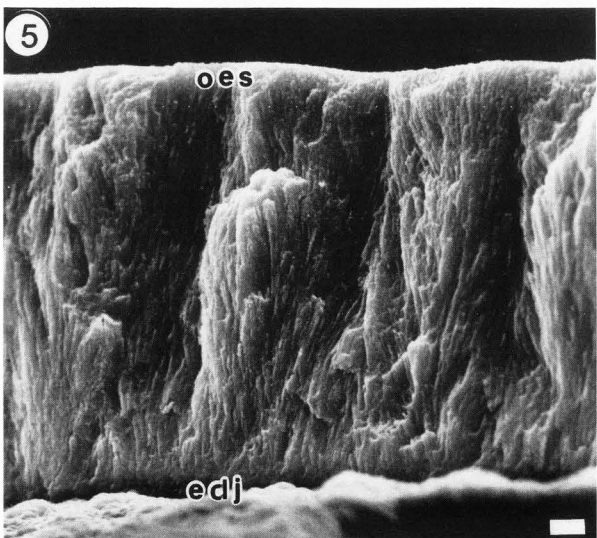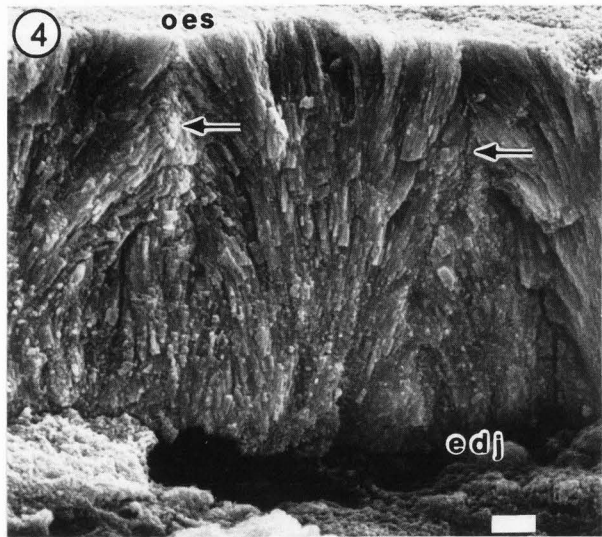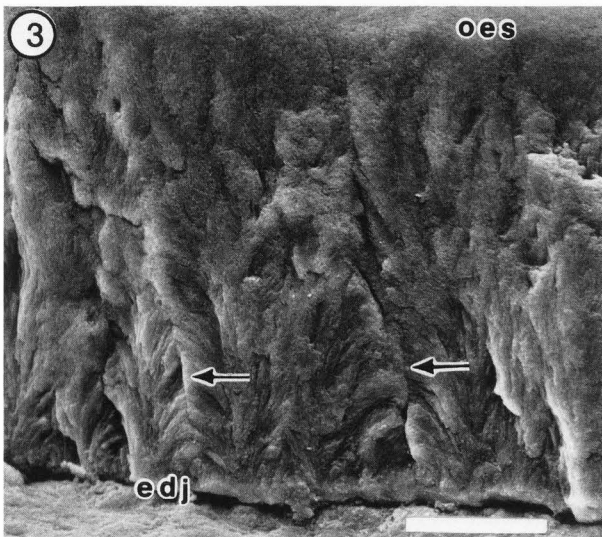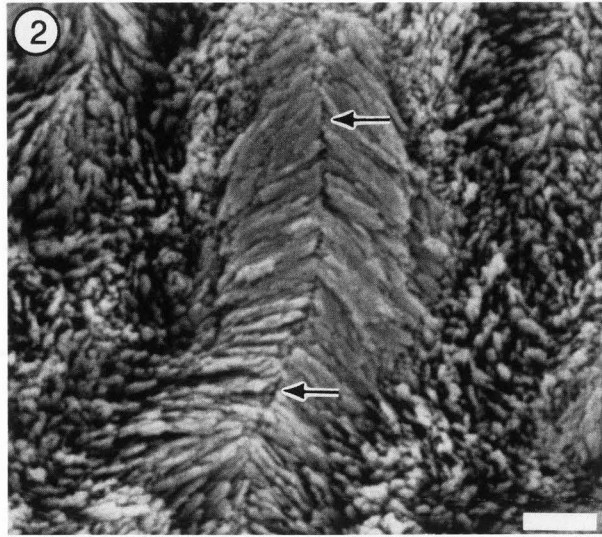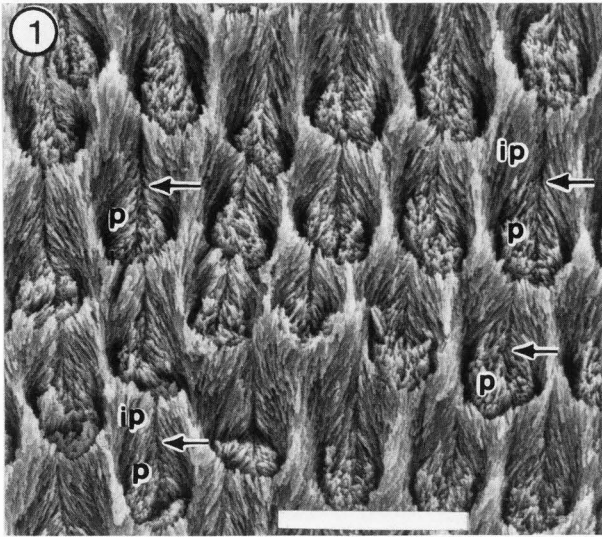
Smilodon californicus, sabretooth felid, Late Pleistocene, Rancho la Brea, Los Angeles, California, U.S.A. One tooth provided by W.A. Akersten, Pocatello, Idaho.

Felis catus, domestic cat.

Where appropriate specimens were available, the enamel was examined both in naturally occurring (fractured or worn) surfaces and in prepared, sectioned surfaces. The natural or existing surfaces were lightly airpolished[TM] prior to etching. The sectioned, polished surfaces were prepared after refluxing the specimens in chloroform/methanol and embedding in methyl methacrylate. All surfaces were lightly etched (1% H_3PO_4 for 5 sec) prior to sputter coating with gold and examined in a JEOL 840 SEM at 15kV. Stereopair images with a tilt angle difference of $10°$ were prepared where appropriate.

Observations

Oligokyphus sp.: Minor linear discontinuities in crystallite orientation are consistently present in the inner two-thirds of the fractured cervical enamel available to us (Fig. 3). The spacing and length of the discontinuities - the term "convergence lines" has been proposed (Lester, 1989b) - are variable, with poorly resolved crystallite groups subtending an angle of approximately $80°$ to the enamel-dentine junction on either side. Close to the enamel-dentine junction, small triangular or cone-like fragments of enamel (with apex towards the outer enamel surface) are fractured out indicating a preferential orientation of crystallites. Overall, there is a clear indication of a preferential massing of crystallite groups in cone-like arrays about each linear feature. In the thinner outer layer of enamel, the crystallites are essentially parallel with each other and perpendicular to the outer surface.

Eozostrodon parvus: The fractured enamel surface is similar to *Oligokyphus* (above), although the enamel available to us is thinner (ca. 10 µm) in our specimens, with the crystallite groups again arranged predominantly in cone-like arrays (Fig. 4). The crystallite groups are mostly vertical close to the enamel-dentine junction but, where organized discontinuously on either side of the convergence line, subtend an angle of approximately $80°$ to the enamel-dentine junction. In places, longitudinal bush-like aggregations (5-6 µm wide) of crystallites may be fractured out to produce a superficial similarity to prisms (Fig. 5). These are, in reality, "pseudoprisms" and are perhaps the structures interpreted as prisms by Grine et al. (1979) in a tangential surface of rather heavily etched *Eozostrodon* material (see Discussion).

Haldanodon expectatus: There is a greater degree of repetitive organization of crystallite groups in this specimen than in either *Oligokyphus* or *Eozostrodon*. Ordered patterns resulting from discontinuity in crystallite orientation are visible in both longitudinally fractured (Fig. 6) and polished (Fig. 7) surfaces. With progressive airpolishing[TM], a flat surface was thrown into relief reflecting a high level of pseudoprismatic organization (Fig. 8).

There are three "layers" in these enamel surfaces; the innermost being the thinnest and consisting of essentially parallel crystallite groups oriented vertically to the enamel-dentine junction. The most obvious minor discontinuities occur in the bulk of the middle enamel as radial convergence lines at which the crystallites subtend an acute angle to the enamel-dentine junction (Fig. 9): again, we interpret the arrangement of crystallite groups fanning out to the convergence lines on either side as pseudoprismatic. In the outer enamel, the crystallites are generally perpendicular to the outer surface: this simpler orientation would be consistent with a flat secretory surface to the ameloblast. The change of structure within the enamel indicates change in morphology of the Tomes' processes during enamel formation (Boyde, 1964; 1976; 1989; and see Discussion).

Attempts to visualize crystallite orientation in surfaces of *Haldanodon* enamel where the sectioned surface did not include the longitudinal axis of the majority of crystallites were generally unsuccessful. This highlights a general and real difficulty in resolving pseudoprismatic

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Fig. 7. *Haldanodon expectatus* (docodont mammal) enamel: longitudinal section of polished, etched, cuspal region showing recurring convergence lines (at arrows) and pseudoprismatic pattern in middle third enamel (edj - enamel-dentine junction; oes - outer enamel surface). Bar = 10 µm.
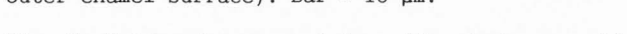
Fig. 8. *Haldanodon expectatus* (docodont mammal) enamel: longitudinal section of cuspal region airpolished to throw convergence lines (at arrows) and pseudoprismatic structure into relief (oes - outer enamel surface; asterisk locates middle of enlargement at Fig. 9). Bar = 10 µm.
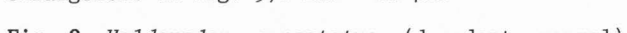
Fig. 9. *Haldanodon expectatus* (docodont mammal) enamel - enlargement about asterisked area in Fig. 8 - to show detail of orientation of crystallites about convergence lines (at arrows). The perceived units (between arrows) are pseudoprisms. Bar = 10 µm.

Fig. 10. *Haldanodon expectatus* (docodont mammal) enamel: polished and etched transverse section from near enamel-dentine junction region showing an array of tubules (at arrows) that would result from ameloblast cytoplasm extensions from the tips of conical Tomes' processes. Bar = 1 µm.

Fig. 11. *Haldanodon expectatus* (docodont mammal) enamel: oblique transverse section of full thickness showing regular cell-based pattern thrown into relief by air-polishing. Asterisk locates enlargement at Fig. 12 (edj - enamel-dentine junction; oes - outer enamel surface). Bar = 10 µm.

Fig. 12. *Haldanodon expectatus* (docodont mammal) enamel - enlargement of Fig. 11 (asterisk locates same feature) - showing recurring pseudoprismatic structure in oblique transverse section theoretically related to conical Tomes' processes during development. Bar = 10 µm.

enamel structure in transversely sectioned surfaces by the more conventional SEM method of polishing and etching. A repetitive unit 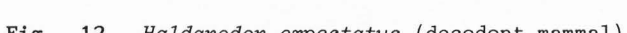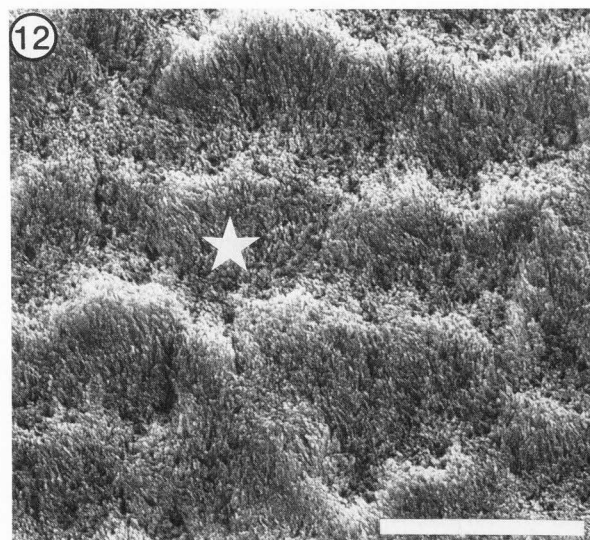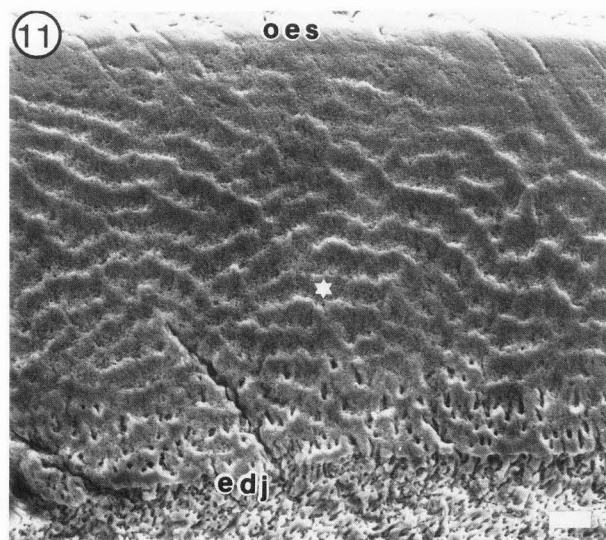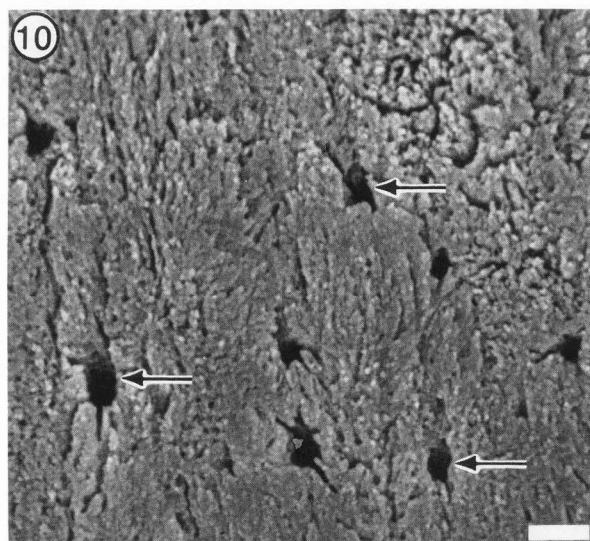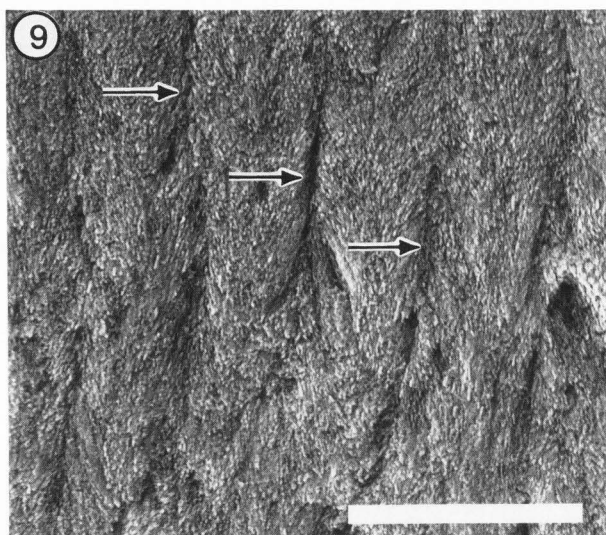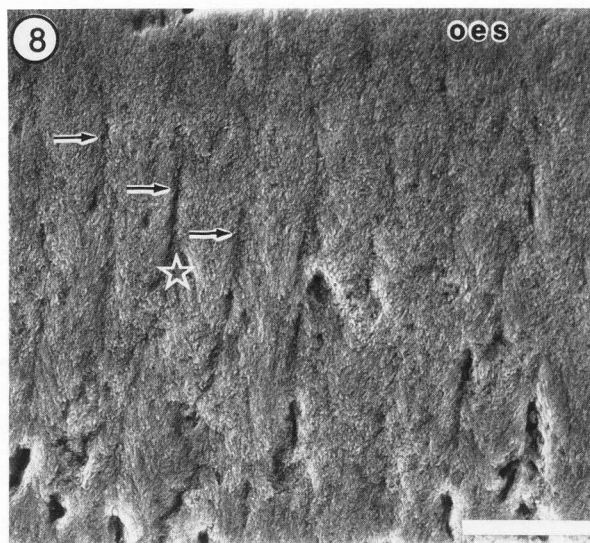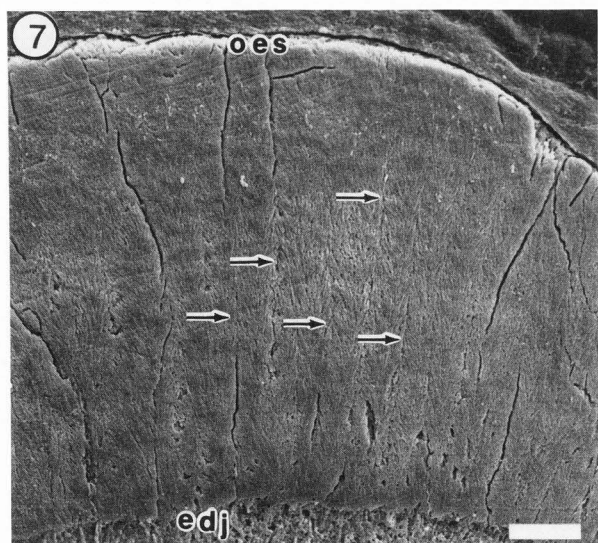of sorts could be found, however, in transverse sections of the inner enamel prepared in this way, where tubules appeared to act as a central focus for crystallite orientation (Fig. 10). In the middle bulk of the enamel, it was possible to express a repetitive structure by airpolishing^{TM} where oblique or tangential sections captured the longitudinal axis of a majority of crystallites (Figs. 11, 12). The pattern could be interpreted as hexagonally packed, ameloblast-related (av. diam. 4-5 µm), and the result of the influence of short, cone-shaped Tomes' processes during development to form pseudoprisms (see Discussion). The crystallites meet in the centre at an angle, indicating that the convergence line is the centre of the unit cell secretory territory (Figs. 37, 40A).

Eupantothere: This enamel combines in a very elemental way, a pseudoprismatic structure with what we would term a partial prismatic structure; the latter expressed by short, rudimentary major planar discontinuities (or "short arcs of prism sheaths" (Osborn and Hillman, 1979)) (Figs. 13, 14, 15). The combination can be appreciated in three dimensions by viewing a stereopair of a (oblique longitudinal) fractured surface of coronal enamel in which small but discrete, well-spaced, partial prisms emerge from a well organized bulk of pseudoprismatic enamel (Fig. 13). In other words, there is here a coexistence of two basic domains: prism, albeit partial, and pseudoprism; with the seam feature common to both.

In polished surfaces, the partial prisms again appear to emerge from between pseudoprismatic columns (Figs. 14, 15) in the inner half to two-thirds of the enamel. The partial prisms are expressed here by rudimentary or partial major planar discontinuities in the form of very incomplete horseshoes facing away from the enamel-dentine junction, each in association at its open end with a seam. The seam, now subdividing the pseudoprismatic domain, has replaced the convergence line as the dominant feature of that domain (cf. *Haldanodon*). The outer layer of enamel is aprismatic (Fig. 14).

The short major planar discontinuities, and hence the partial prisms, do not appear in the enamel close to the enamel-dentine junction. Progressive transverse sectioning disclosed instead another kind of repetitive unit in the first-deposited enamel in the form of hexagonally packed domains (ca. 5-7 µm diam.) (Figs. 16 and 17). Away from the junction, transversely sectioned major planar discontinuities, representing at least very rudimentary prisms, begin to appear; each discontinuity being minimal in extent and little more than a slightly curved line (some concave and some convex) with short extensions at either end (Fig. 18). These short extensions often display a slight terminal enlargement of the etched discontinuity (see also Lester and Hand, 1987). A seam (minor planar discontinuity) occurs in association with some of the major planar discontinuities oriented perpendicularly to, and at the mid-region of the major feature. Crystallite groups focussing inwards from the ends of the boundaries meet and, in so doing, constitute the seam (Fig. 19).

Some fractured enamel surfaces of eupantothere enamel are initially very confusing and difficult to interpret in that there is an obvious recurring pattern but not of prisms (Fig. 20). The difficulty in interpretation arises because the major planar discontinuities are very short and, as a result, quite far from actually completing a recognizable domain in the normal sense of providing for the viewer a convenient, total, recognizable prism. The general impression from this kind of surface is one of a complex network of branching and interlocking enamel domains: these are in fact "fractured out" pseudoprismatic domains that may initially be confused in some areas with prisms if the problem is only examined superficially (Figs. 21 and 22). As a direct result of the short major planar discontinuities, the bodies of the partial prisms are very much a secondary contributor to the bulk of this enamel and, in this surface, run relatively inconspicuously and at an angle to the major and continuous pseudoprismatic phase.

The difference between the appearance in Figs. 21 and 22 is that the fracture line has involved the major discontinuity (partial "prism sheath") in both, with the seam included in Fig. 22 but not in Fig. 21. This complex fracture site can be
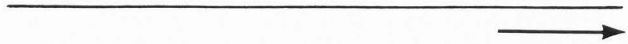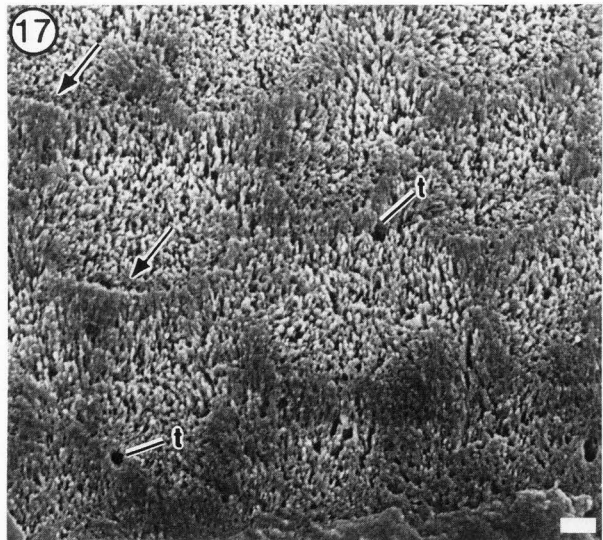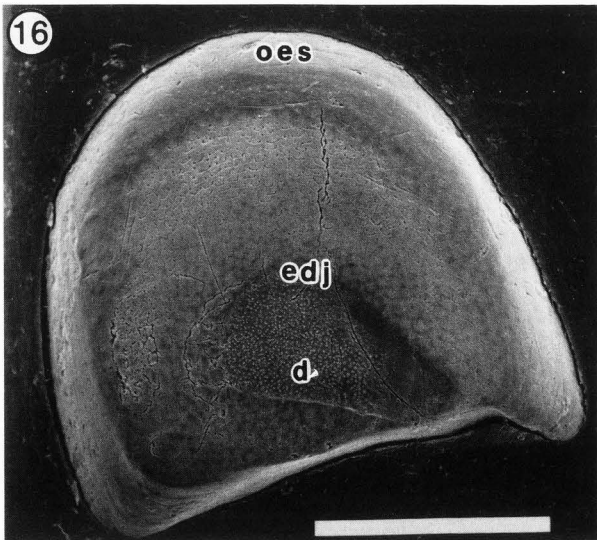

Fig. 13. Eupantothere (dryolestid mammal) enamel - stereopair of an oblique longitudinal fracture of cuspal region, etched, showing discrete, well-separated, partial enamel prisms (p) emerging in association with seams (at arrows) from within the more dominant pseudoprismatic elements (pp) (edj - enamel-dentine junction). This stereopair (tilt angle = 10°) and Figs. 14 and 15 represent, in a sense, the "birth" of the prism from within the pseudoprismatic domain. Bar = 10 µm.

Fig. 14. Eupanthothere (dryolestid mammal) enamel: polished, etched, longitudinal section of cuspal region showing obliquely sectioned partial prisms (p) in asociation with seams (at arrows) arising from between pseudoprismatic elements (pp) (edj - enamel-dentine junction; oes - outer enamel surface). Bar = 10 µm.

Fig. 15. Eupantothere (dryolestid mammal) enamel - enlargement of lower left central area in Fig. 14 - showing detail of seams (at arrows); pseudoprism (pp); and prisms (p). Bar = 1 µm.

Fig. 16. Eupantothere (dryolestid mammal) enamel: polished and etched transverse section of tooth crown showing distribution of enamel and dentine. Note recurring hexagonally packed pseudoprismatic elements, especially near enamel-dentine junction (edj) (d - dentine; oes - outer enamel surface). Bar = 100 µm.

Fig. 17. Eupantothere (dryolestid mammal) enamel: enlarged from Fig. 16, showing transversely sectioned cell-based pseudoprismatic elements near the enamel-dentine junction (edj). Note earliest indications of short major planar discontinuities (partial prism borders) at arrows (t - tubules). Bar = 1 µm.
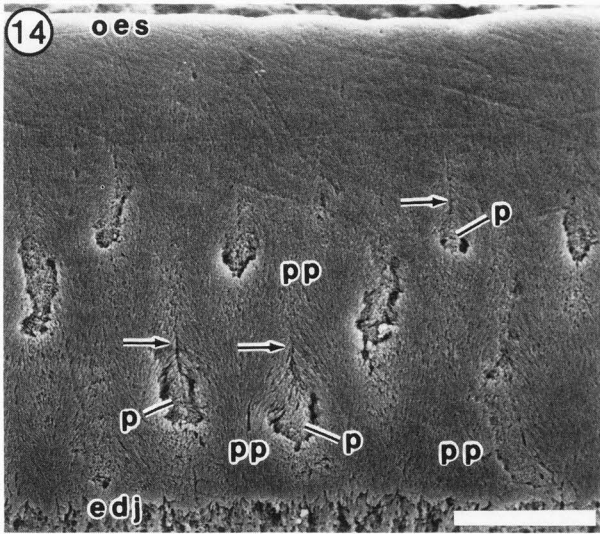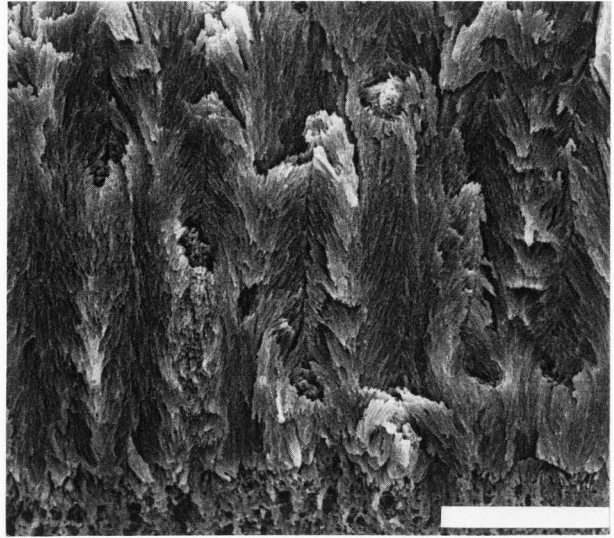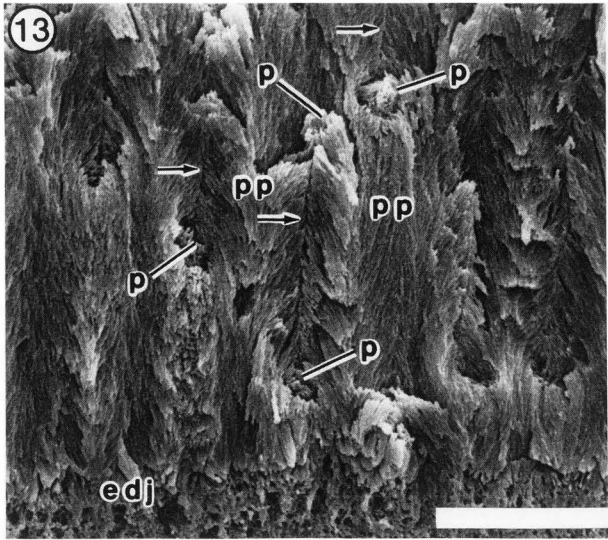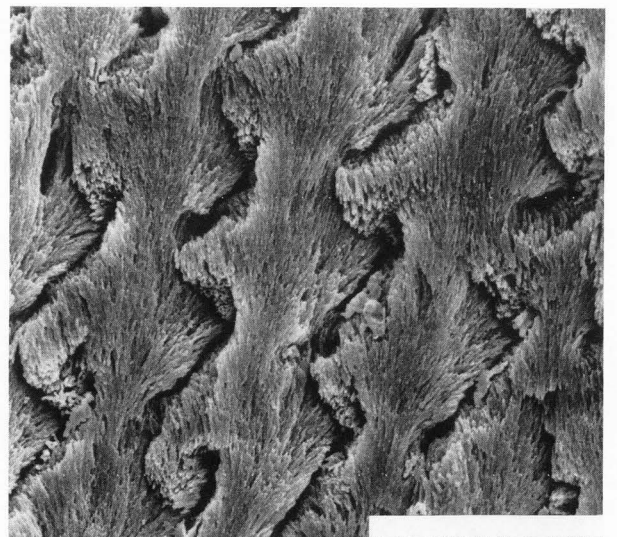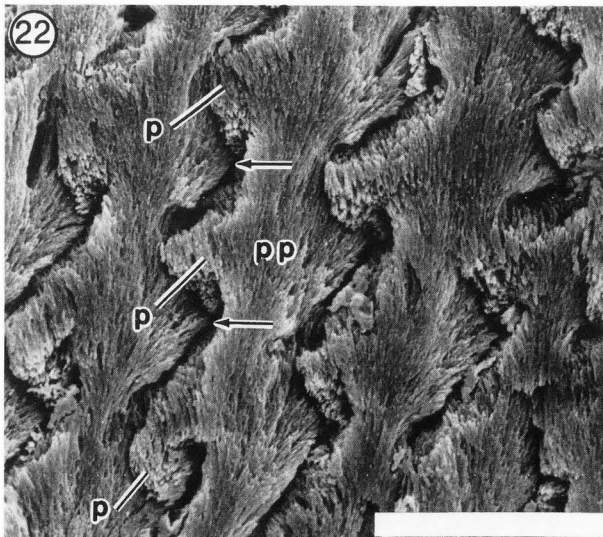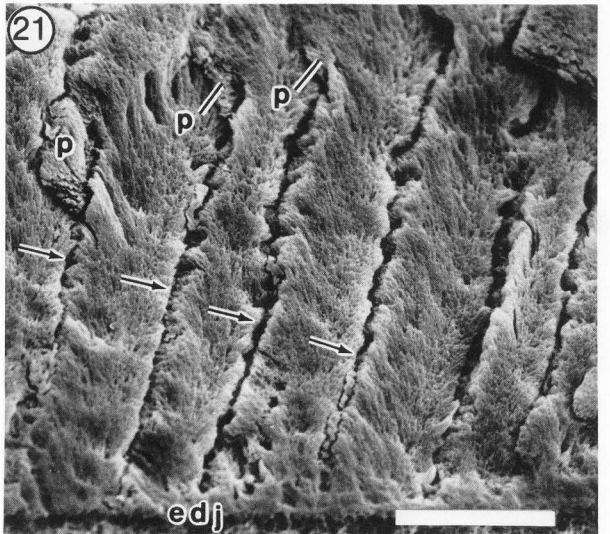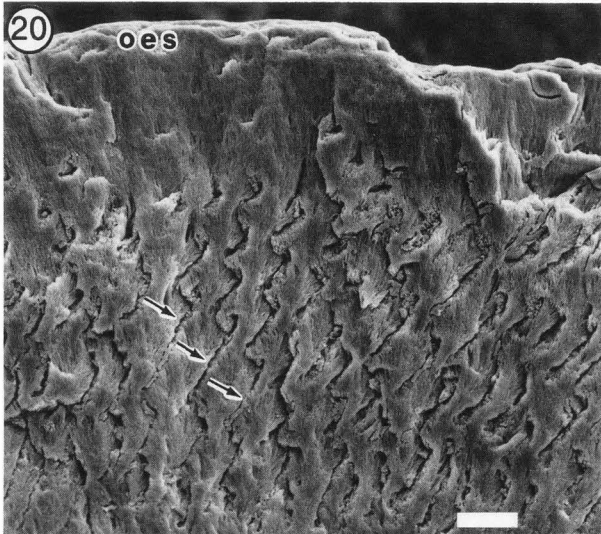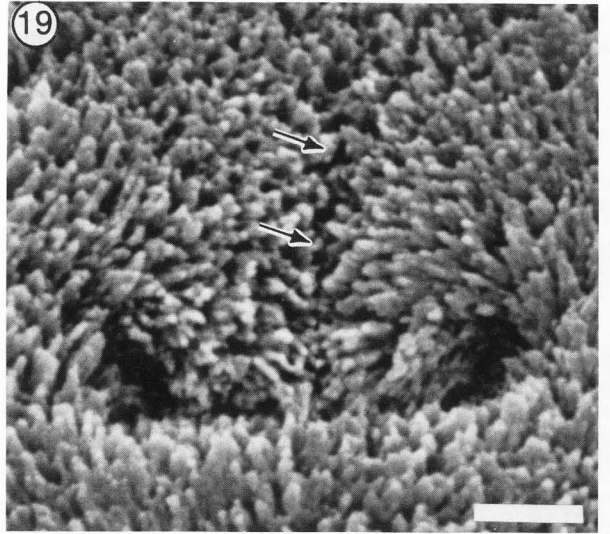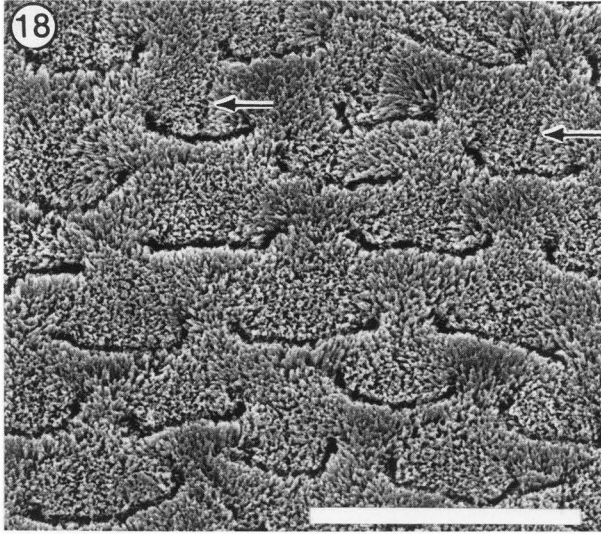
Fig. 18. Eupantothere (dryolestid mammal) enamel: enlargement of middle third enamel from Fig. 17, showing short major planar discontinuities (partial prism boundaries), some in association with seams (at arrows). The planar discontinuities do not envelop a "complete" domain (prism) in the way we have come to anticipate in mammals. Bar = 10 µm.

Fig. 19. Eupantothere (dryolestid mammal) enamel: showing a higher magnification of the crystallite orientation about the attenuated major planar discontinuity and associated seam (at arrows) in transversely sectioned inner middle third enamel. Note the enlargement at either end of the planar discontinuity representing the sites of most significant change of contour in the developing surface. Bar = 1 µm.

Fig. 20. Eupantothere (dryolestid mammal) enamel: etched, oblique longitudinal fracture of cuspal region exposing the principal pseudoprismatic elements which normally in higher mammals would be dominated by prisms. The major planar discontinuities (prism boundaries) here are partial and are either fractured longitudinally (at arrows and see Fig. 21) or partly transversely (see Fig. 22). Figs. 38 and 40B help explain the complex fracture plane (oes - outer enamel surface). Figs. 21 and 22 are higher magnifications. Bar = 10 µm.

Fig. 21. Eupantothere (dryolestid mammal) enamel: enlargement of extreme part of lower left of Fig. 20, showing longitudinal fracture along major planar discontinuities (in middle at arrows) and exposing transversely fractured partial prisms (p) at top - see also Fig. 38. Major planar discontinuities (partial prism boundaries) are at arrows (edj - enamel-dentine junction). Bar = 10 µm.

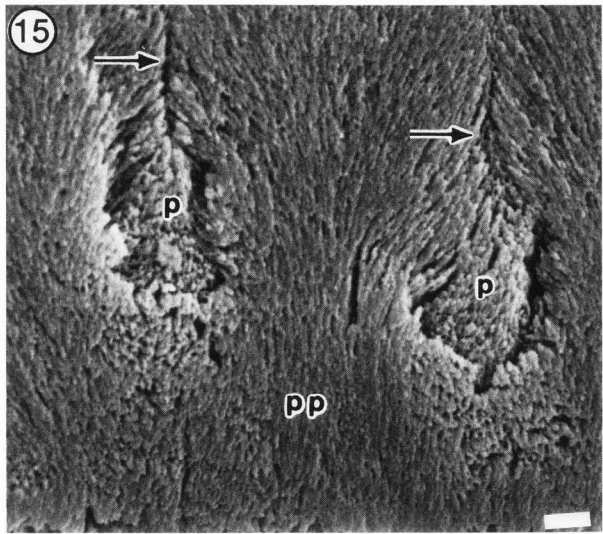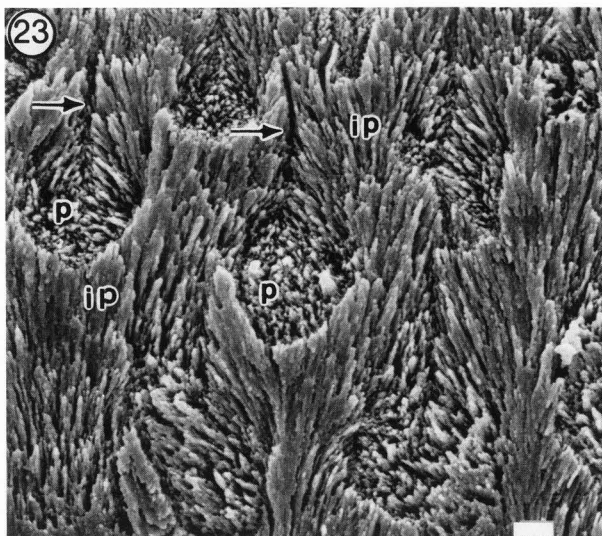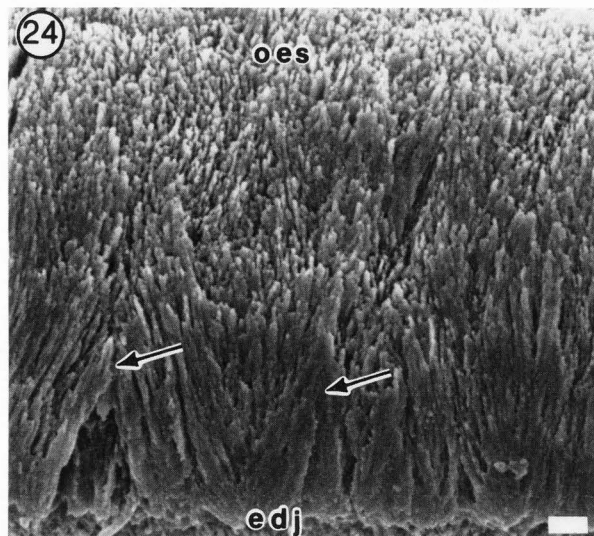**Fig. 22.** Eupantothere (dryolestid mammal) enamel: stereopair enlargement of part of Fig. 20 immediately above arrows - showing fracturing out of major pseudoprismatic component (pp) between the minor partial prism component (p). The partial prisms run obliquely into the specimen surface left to right. The fracture line has included part of the major planar discontinuity (partial prism boundary) - see also Fig. 38. Stereopair tilt angle = 10°. Bar = 10 µm.

Fig. 23. *Amphiperatherium* sp. (didelphid marsupial) enamel: polished, etched, transerve section of cuspal region with middle region showing horseshoe-shaped prisms (p) in association with a seam (at arrows) at their open end and contiguous with the interprismatic phase (ip). Bar = 1 µm.

Fig. 24. *Amphiperatherium* sp. (didelphid marsupial) enamel: longitudinal section of polished, etched, cervical region showing loss of prismatic structure but retention of convergence lines (at arrows) where thickness of enamel is reduced to 10 µm (edj - enamel-dentine junction; oes - outer enamel surface). Bar = 1 µm.

clarified by reference to a three dimensional diagram constructed to help explain some developmental aspects of this interesting enamel structure (see Discussion and Figs. 38, 40b).

Amphiperatherium sp.: Both fractured and sectioned surfaces (Fig. 23) display a consistent and conspicuous seam in association with horseshoe-shaped prisms. Prisms are dominant in the inner part of the enamel and fade away in the outer part. Cervically, where the enamel reduces to approximately 17 µm thickness, the prisms are lost although seam (? convergence line) formation persists (Fig. 24) in the same way as reported for *Desmodus* (Lester et al., 1988).

Hassianycteris: The prisms are closer packed than in the didelphid and the development of seams, although discernible, is not nearly as marked (Figs. 25, 26) as in the fossil marsupial. It is a little surprising to us that this feature is not stronger and that the prism centres are so close in this fossil bat (for comparison with other fossil and Recent bats, see Lester and Hand, 1987; Lester et al., 1988). The pseudoprismatic element, however, remains very clear in the fractured enamel surface (Fig. 26).

Smilodon californicus: Seams are a very conspicuous feature of this enamel in association with the open end of the horseshoe-shaped prisms, almost to the point of producing bifid prisms (Fig. 27). Fig. 27 shows the seams with the open aspect of the prism horseshoe directed towards the viewer, and Fig. 28 shows the seams with the closed continuous aspect of the prism horseshoe directed towards the viewer. Figs. 29 and 30 demonstrate particularly clearly how the prisms and the seams end in the outer enamel: the prismatic enamel gives way to an intermediate layer of pseudoprismatic enamel, which arises from the interprismatic enamel, that itself gives way to a very thin outer layer of aprismatic enamel.

Felis catus: The seam feature is present to a variable degree in association with transversely and longitudinally sectioned prisms (Figs. 31 and 32 respectively). Where the seams occur, the appearance is similar to that in the eupantothere where the crystallite groups radiate towards the seam from the ends of the major planar discontinuity (cf. Figs. 13 and 31). As with *Smilodon*, there is towards the outer enamel surface an intermediate zone of pseudoprismatic enamel between the inner prismatic and the outer aprismatic layers (Fig. 33). It is clearly the pseudoprismatic or interprismatic phase that emerges here and envelops the ends of the prisms but retains the seam (? convergence line) until it, too, is lost in the external (aprismatic) enamel.

Although Hunter-Schreger bands are expressed in both *Smilodon* and *Felis*, the bands are both more numerous and organized in the latter.

Discussion

The mammalian genera examined here belong to very different groups necessarily representing very different evolutionary levels. In sum however, they do offer a working model for the evolution of mammalian enamel in terms of the differentiation of the secretory surface of the ameloblast and the resultant increase in complexity of the orientation of crystallites over geological time. Carlson (1989) has independently taken a similar approach.

Minor crystallite orientation discontinuities

A significant finding of this study is that minor discontinuities in crystallite orientation are a consistent characteristic of enamel structure in samples spanning 200×10^6 years.

Convergence Lines (210 Ma). In an advanced therapsid (*Oligokyphus* - Fig. 3) and in an early mammal (*Eozostrodon* - Fig. 4) from the Late Triassic at about 210 Ma, the enamel is discontinuous with discrete, sometimes well separated, columnar, fan-like arrays of crystallites. The linear discontinuity (convergence line (Lester, 1989b)) within these arrays, where the crystallites meet to subtend an angle towards the enameldentine junction, is the cell-based "centre" of these structures in a developmental sense. We assume this pattern is formed by ameloblasts having a simple, cone-shaped, secretory surface and that the tip of the cone results in the convergence line (see below). We would classify these enamels as irregularly pseudoprismatic despite the use of the term "prismatic" by Dauphin and Jaeger (1987) and Dauphin (1988) for *Oligokyphus* and by

Grine et al. (1979) and Osborn and Hillman (1979) for *Eozostrodon*. Carlson and Bartels (1986) and Carlson (1989) have come to a similar conclusion.

Convergence Lines (175 Ma). At about 175 Ma, the Late Jurassic *Haldanodon* (Fig. 8) displays a discontinuous and layered enamel. The discontinuity, most obvious within the widest and middle layer, is again linear but more regular and discrete when viewed in its longitudinal axis. These discontinuities too, we see as convergence lines and distinguish them from seams (Lester and Hand, 1987; Lester et al., 1988; Lester and Boyde, 1987) and prism boundaries, both of which manifest themselves in two dimensions in both longitudinal and transverse planes. We conclude that convergence lines are fundamental to and characteristic of the enamel of *Haldanodon*, which we would classify as regularly pseudoprismatic.

Seams (175 Ma). The dryolestid eupantothere (Figs. 18, 20) was studied from the same geological formation (175 Ma) that produced *Haldanodon*. In the eupantothere, one could regard the convergence line (minor linear discontinuity) of *Haldanodon* as being further developed to become a seam (minor planar discontinuity) concomitant

Fig. 25. *Hassianycteris messelensis* (archeonycterid chiropteran) enamel: transverse section of cuspal region, polished and etched, showing transversely sectioned horseshoe prisms (p) closepacked and in association with seams (at arrows). Bar = 1 µm.

Fig. 26. *Hassianycteris messelensis* (palaeochiropteran) enamel: etched, oblique longitudinal fracture at enamel-dentine junction (edj), showing fractured prisms (p) in association with seams (at arrows). Bar = 10 µm.

Fig. 27. *Smilodon californicus* (sabretooth felid) enamel: polished, etched, transversely sectioned prisms showing strong development of seam (at arrows) at the open ends of the horseshoe-shaped prisms (p) which are towards the viewer (ip - interprism) (cf. Fig. 28). Bar = 1 µm.

Fig. 28. *Smilodon californicus* (sabretooth felid) enamel: polished, etched, oblique transverse section of prisms showing seams (at arrows) at the open ends of the prisms (p) which are directed away from the viewer (ip - interprism) (cf. Fig. 27). Bar = 10 µm.

Fig. 29. *Smilodon californicus* (sabretooth felid) enamel: longitudinal, polished, etched, section showing prisms (p) ending towards the outer enamel surface (oes) giving way, first to pseudoprismatic (pp) and then to aprismatic (ap) outer enamel. Enlarged in Fig. 30. Bar = 10 µm.

Fig. 30. *Smilodon californicus* (sabretooth felid) enamel: enlargement of area immediately above the two labelled prisms in Fig. 29. As the prisms (p) end, the seams continue as convergence lines (at arrows), characteristic of pseudoprismatic enamel (pp), until it too ends in a thin surface layer of aprismatic (continuous) enamel. Bar = 10 µm.
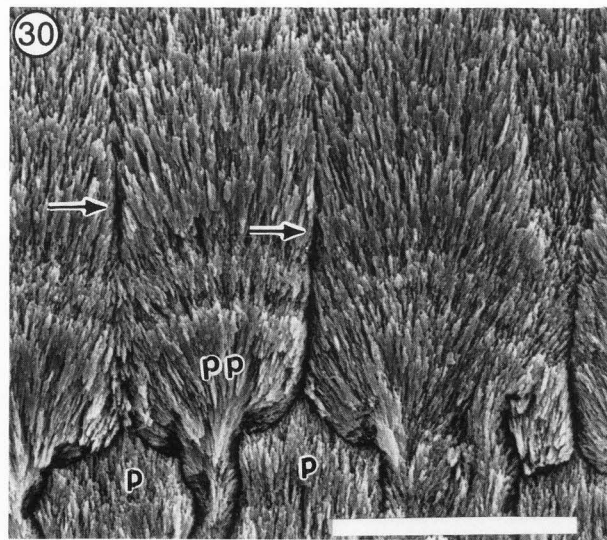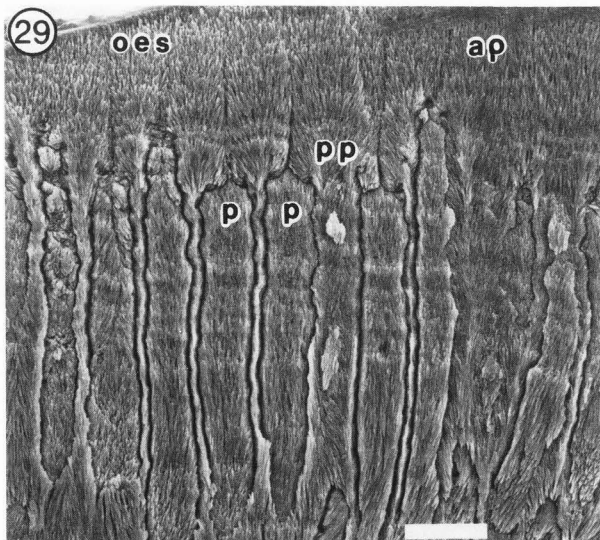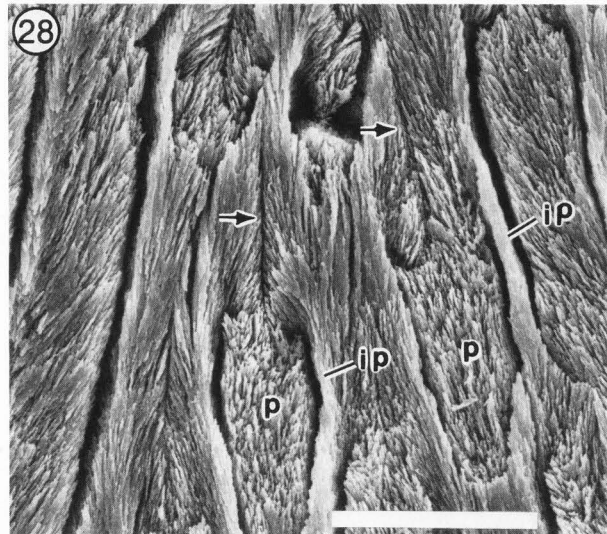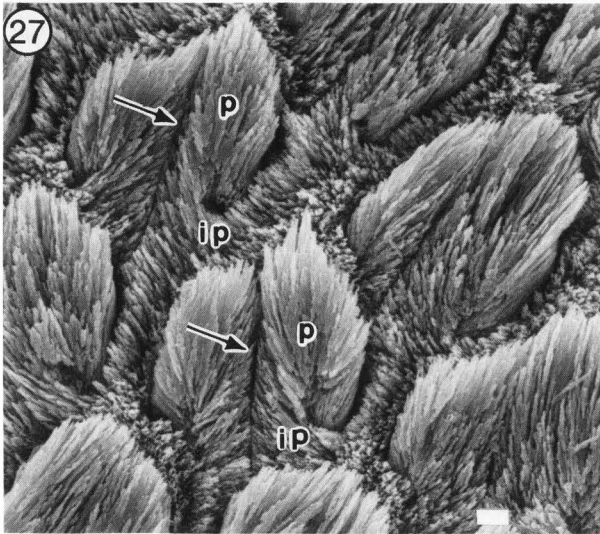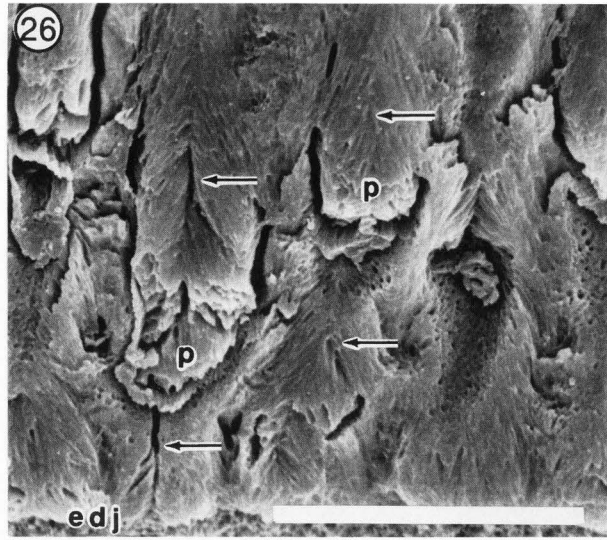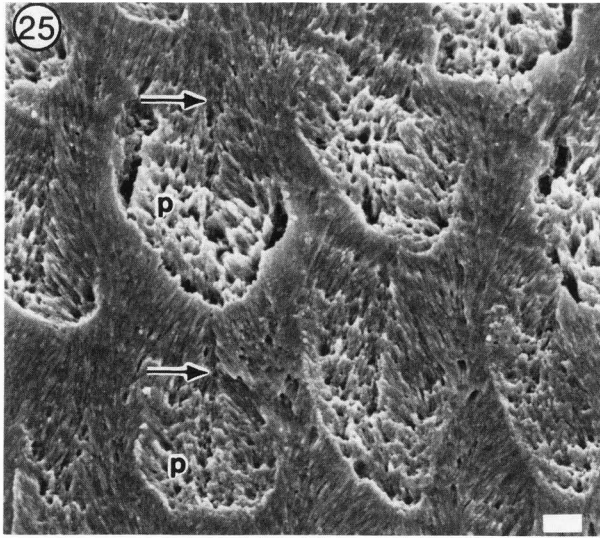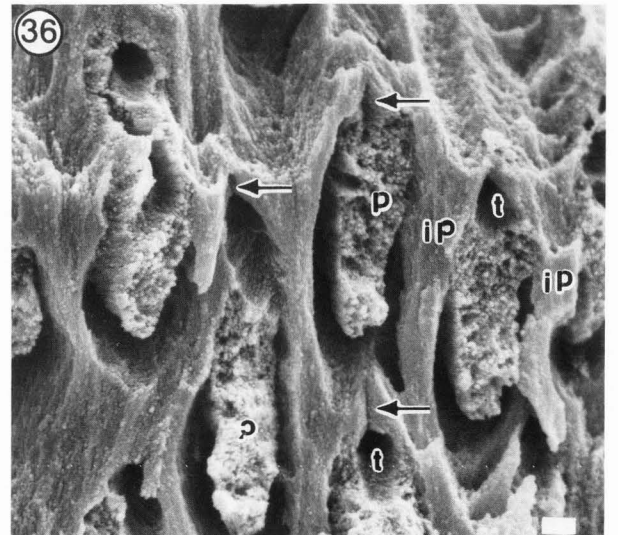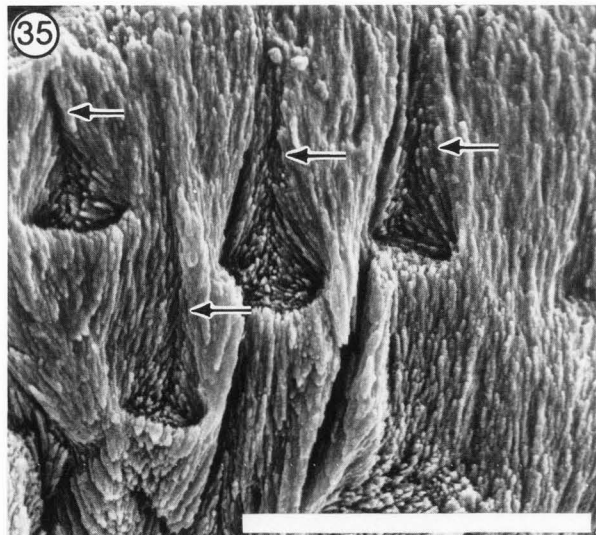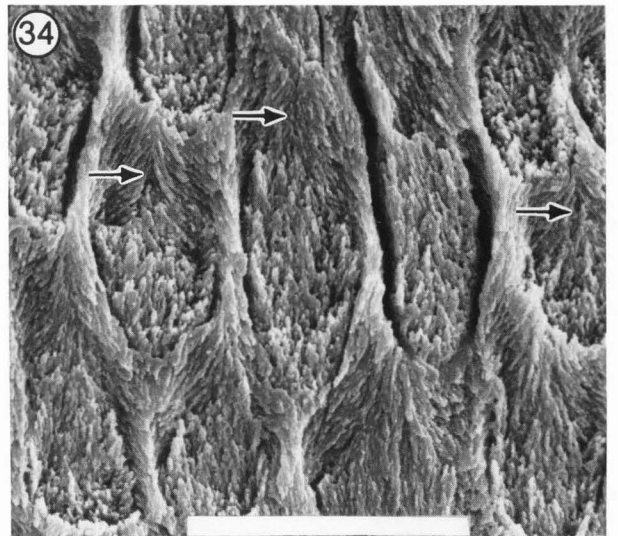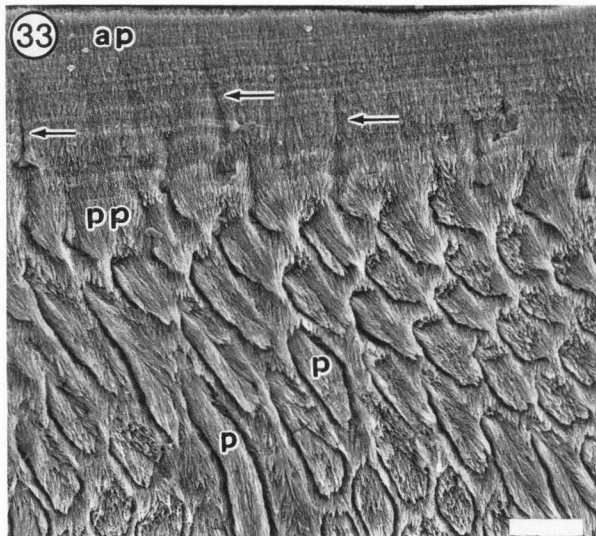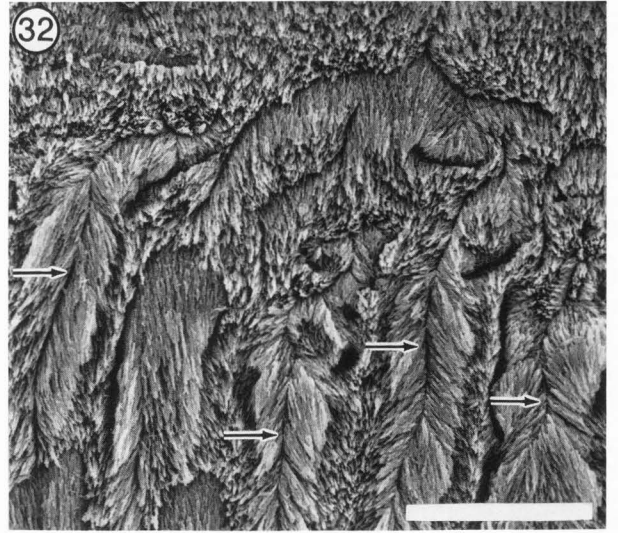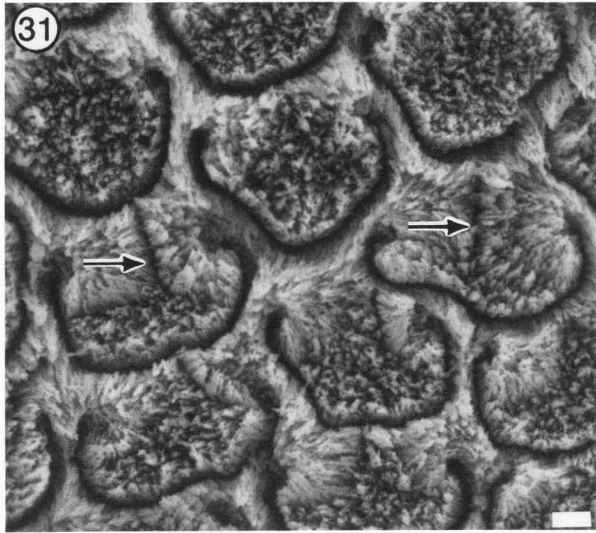
with the appearance of an often extremely short, rudimentary and, in transverse section, attenuated major planar discontinuity. The seam subdivides the pseudoprismatic domain in a regular, recurring way. Thus, according to the fossil record, a particular variety of prismatic enamel defined by rudimentary or partial major planar discontinuities and forming what might be described as "partial" prisms in association with seams, is present in the dryolestids of the Late Jurassic.

Seams (50 - 30 Ma and present). We show here also that seams persist in the Tertiary (50 - 30 Ma) *Amphiperatherium* (Fig.23) and *Hassianycteris* (Fig. 24), the Pleistocene *Smilodon* (Fig. 26) and the extant *Felis catus* (Fig. 31) to coexist with what is generally regarded as a characteristic development in extent and shape of the major planar discontinuities (prism boundaries). In other words, seams and substantive prisms coexist in these four genera.

Seams have been shown previously to exist in conjunction with horseshoe-shaped prisms in the majority of Microchiroptera and a dermopteran (Lester and Hand, 1987; Lester et al., 1988). The exaggerated presence of seams, reported but not illustrated in a palaeoryctid insectivore (*Procerberus*) by Lester and Hand (1987) has since been illustrated and a model for its development proposed (Lester, 1989b). Seams are also present in the Pattern 2 enamel of human deciduous teeth

near the enamel-dentine junction (Fig. 34); in the enamel of an extant Australian marsupial (Fig. 35); and in the enamel of the fossil prototherian, *Obdurodon* (Lester and Archer, 1986) (Fig. 36). The seam is thus a widely occurring, and possibly previously unappreciated, structural characteristic of fossil and extant mammalian enamels (see also Lester, 1989a).

Emergence and Regression of Prisms

There is a structural similarity between what we suspect are the "emerging" poorly expressed partial prisms in the eupantothere, and the "regressing" poorly expressed partial prisms of *Desmodus* (Lester et al., 1988), and see this as a further indication of the evolutionary continuum of enamel. The zoological ubiquity and antiquity of the seam suggests to us that it is a primitive characteristic, possibly antedating, but certainly appearing at the same time as the first indications of a major planar discontinuity or of "partially" prismatic enamel, and one which preferentially survives through the prismatic phase and into the post-prismatic. The dominance of the prism as the structural unit in enamel has undoubtedly overshadowed the continued presence of both the pseudoprismatic component and the seam in mammalian enamel, and has possibly inhibited their wide recognition. Once identifiable prisms are established in an enamel, we tend in normal usage to relegate all else to "interprism" in the description of that enamel (Lester, 1989b). However, given the loss of the prism or parts thereof as a structural unit in the enamel of a particular genus, it seems that the pseudoprismatic component and associated convergence lines either survive, or re-establish their identity, to become the dominant structural features. This can be captured routinely as having occurred within the developmental life cycle of the ameloblast population for one tooth (as in *Smilodon*, Fig. 29). It is likely that the "very simple" prism structure described in the delphinid *Neophocaena* (Ishiyama, 1987) is secondarily reduced, as proposed, but actually pseudoprismatic in form (his Fig. 23).

Developmental diagram for pseudoprismatic enamel

Two, two dimensional developmental models have been proposed independently to account for the formation of pseudoprismatic (pre-prismatic) enamel (Lester, 1988; 1989b; Carlson, 1989). On the basis of known principles (Boyde, 1964, 1965), it is possible to construct a hypothetical three dimensional diagram of the relationship between the developing front and formed pseudoprismatic enamel (Fig. 37). The hexagonal outlines in this construction represent a plan view of the ameloblast cells at their junction with the Tomes' processes. The dots in the middle of the hexagons represent the tips of the pointed (conical) Tomes' process. The contiguous longitudinal faces (1-4) represent formed enamel together with the associated developing front at the section plane indicated (ab, bc, cd, da); note the different widths but generally similar crystallite patterns of the domains at all four sectioned faces. Faces ab and bc only show maximal crystallite convergence because the associated section involves the tip of the Tomes' process. An ameloblast-related "unit" of pseudoprismatic enamel would relate not to the line of convergence so obvious to the eye of the

Fig. 31. *Felis catus* (domestic cat) enamel: polished, etched, transverse section of cuspal region showing transversely sectioned prisms, some of which possess seams (at arrows). Bar = 1 μm.

Fig. 32. *Felis catus* (domestic cat) enamel: polished, etched, longitudinal section towards the outer enamel surface (at top) showing seams (at arrows) in association with longitudinally sectioned prisms (p). Bar = 10 μm.

Fig. 33. *Felis catus* (domestic cat) enamel: polished, etched, oblique longitudinal section; showing outer enamel region (surface at top) with prisms (p) ending to give way to a pseudoprismatic (pp) and then an aprismatic (ap) outer layer. Seams and/or convergence lines at arrows. Bar = 10 μm.

Fig. 34. Human deciduous enamel: etched, polished, oblique transverse section near enamel-dentine junction showing seams (at arrows) in association with horseshoe-shaped prisms. Bar = 10 μm.

Fig. 35. *Tarsipes rostratus* (extant metatherian) enamel: oblique transverse section, etched, showing seams (at arrows) in association with prism ends at the outer enamel surface (at top). Bar = 10 μm.

Fig. 36. *Obdurodon insignis* (fossil prototherian) enamel: oblique transverse section near enamel-dentine junction showing grossly etched horseshoe-shaped prisms (p) in association with tubules (t) and seams (at arrows) (ip - interprism). Bar = 1 μm.
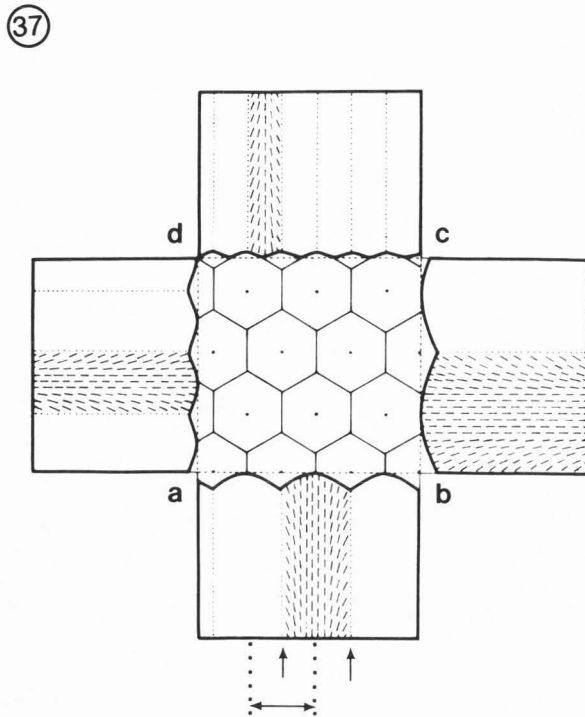
Fig. 37. Three dimensional diagram of the proposed relationship between the developing (mineralizing) front and formed pseudoprismatic enamel. The model is after Boyde (1964, 1965). The hexagonal outlines represent a plan view of the ameloblast cells at their junction with the Tomes' processes. The dots in the middle of the hexagons represent the tips of the pointed (conical) Tomes' process. The contiguous longitudinal faces represent formed enamel together with the associated developing front at the section plane indicated (ab, bc, cd, da). Note the different widths but generally similar crystallite patterns of the domains at all four sectioned faces. Faces ab and bc only show maximal crystallite convergence because the associated section involves the tip of the Tomes' process. An ameloblast-related "unit" of pseudoprismatic enamel (at horizontal arrow) would relate not to the line of <u>convergence</u> (at vertical arrows) but to the plane of <u>divergence</u> of crystallite groups corresponding to the peaks of the developing front between the Tomes' process (see ab) (see also Fig. 38).

Fig. 38. A three dimensional diagram after Boyde (1964, 1965) representing the development of eupantothere enamel - the diagram has been inverted for better comparison with the photomicrographs. Face (ab) shows development of (partial) prism (horizontal arrow) and seam (vertical arrow). Face (bc) shows (partial) prisms which because of the section plane appear to extend the full distance between the (partial) major planar discontinuities: this face is similar to that exposed in the fracture line in Fig. 21.

observer, but to the plane of divergence of crystallite groups corresponding to the convex peaks of the developing front between the Tomes' process (Fig. 37, and see also Lester, 1989b).

Developmental diagram for eupantothere enamel

It is also possible to construct, on the basis of known principles (Boyde, 1964, 1965), a hypothetical three dimensional diagram of the likely relationship between the developing front and formed eupantothere enamel (Fig. 38). The hexagonal outlines again represent a plan view of the ameloblast cell borders at their junction with the Tomes' processes. The relatively short and incomplete horseshoes (major planar discon-

tinuities) represent the junction of the wall and floor of each of the Tomes' process pits in the developing enamel front. The short vertical lines represent the longitudinal groove in the developing front of the sloping floor wall of the Tomes' process pits. The four longitudinal faces arranged around the developing front represent sectioned, formed enamel together with the corresponding section of the developing front on the section plane indicated (ab, bc, cd and da). The block can be "reconstructed" by folding along the dotted lines. Section ab produces two apparent prisms with a seam dividing the apparent interprismatic (? pseudoprismatic) enamel. Section bc produces longitudinal sections of what are, in reality, only partial prisms combined with a significant pseudoprismatic component.

The complex appearance of eupantothere enamel shown in Figs. 20-22 can be explained by envisaging vertical fracture planes through the hexagonal grid: for Fig. 21, directly across the major planar discontinuities to include the seams (see sectioned face bc); and, for Fig. 22, diverted along half the extent of each major planar discontinuity to include the seams.
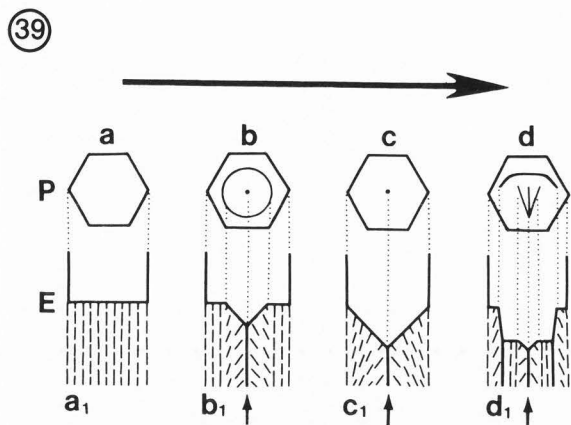
Fig. 39. Diagrams a, b, c and d represent proposed consecutive stages (in direction of large arrow) in the increasing complexity of the evolving Tomes' process over geological time. The hexagonal outline in each represents a plan (P) view of the Tomes' process and its junction with the ameloblast cell body. Below this is projected an elevation view (E) of each Tomes' process and its proposed relationship to the crystallites in the developing enamel (a_1, b_1, c_1, d_1). Diagram a: aprismatic (continuous) enamel; b: pseudoprismatic enamel (as in *Oligokyphus* and *Eozostrodon*; c: pseudoprismatic enamel (as in *Haldanodon*); and d: partially prismatic enamel (as in eupantothere). Vertical arrows indicate convergence line in b_1, and c_1, and seam in d_1.

"Pinnate" vs. "Pre-prismatic" vs. "Pseudoprismatic" vs. "Prismatic"

Kuehneotherium and *Haramiya*. There is conflict and confusion in the literature with regard to terminology for enamel which is not truly prismatic; that is to say, with clearly identifiable prismatic and interprismatic components. For example, Sigogneau-Russell et al. (1984) and Frank et al. (1984), in *Kuehneotherium* and *Haramiya*, respectively, described the enamel as "pre-prismatic" and the crystallite orientation as "pinnate" but then went on in their account to describe "prisms". In the "pinnate" two dimensional picture of Frank et al. (1984; their Figs. 2 and 3), they saw the centres of the "prisms" where we would see the margins of the cell-based pseudoprismatic units. The two dimensional picture is naturally difficult to interpret and a little confusing; three dimensional reconstruction of ameloblast and crystallite orientation allows a better appreciation of the definition of the secretory territories of the ameloblasts for pseudoprismatic enamel (Fig. 37 and Lester, 1989b).

Eozostrodon. Moss and Kermack (1967) and Moss (1969) studied *Eozostrodon* (using the name *Morganucodon*) and called this early enamel "pseudoprismatic" because of the lack of distinct prisms. Poole (1956) carefully described cylindrical domains in the enamel of some synapsid reptiles not separated by an interprismatic component. His use of the term "pseudo-prism" was rejected by Osborn and Hillman (1979), although essentially
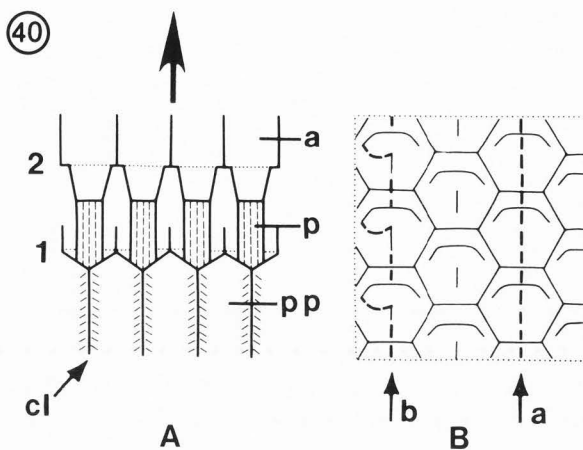

Fig. 40A. A diagram to help in the consideration of pseudoprismatic as opposed to prismatic enamel. Vertical arrow represents direction of movement of ameloblasts (a). At horizontal level 1, cone-shaped Tomes' processes form pseudoprismatic enamel (pp). The convergence line (cl) is related to the tip of the Tomes' process but does not represent the ameloblast-related unit of enamel (see Fig. 38). At horizontal level 2, a battlements plane of Tomes' processes produces prisms (p). The prisms represent an ameloblast-related unit and would, with their seams, be aligned in the direction of the path of the ameloblasts parallel with the convergence lines of the pseudoprismatic enamel.

Fig. 40B. Diagram of developing surface of eupantothere enamel (after Fig. 38 but inverted) to help explain the appearance of the fractured faces in Figs. 20-22. Fracture line (a) intersects the short major planar discontinuities and would account for the appearance in Fig. 21. Fracture line (b) includes one half of the major planar discontinuities, and therefore displays the "partial" prism which would account for the appearance in Fig. 22.

their description of the structural unit was the same. In our view, the "cylinders" of Poole (1956) and the structure deduced by Osborn and Hillman (1979) almost certainly equate - it is worth noting the consistency in these descriptions despite the different terminology. Grine et al. (1979) interpreted *Eozostrodon* enamel as "prismatic" and the "prisms" as hexagonal and circular in transverse section. We classify this type of enamel differentiation, found as early as the Late Triassic, as pseudoprismatic (see also Carlson and Bartels, 1986; Carlson, 1989).

Haldanodon. There is a major gap of up to 50 Ma in the fossil record of Mesozoic mammals between the Late Triassic and the Late Jurassic. Nevertheless, *Haldanodon*, a docodont mammal, retains the pseudoprismatic structure even when differentiation into different layers within the enamel seems to be more complete and complex than in the earlier forms. Moss (1969) investigated the genus *Docodon* from the Upper Jurassic Morrison Formation (U.S.A.) and called the enamel "continuous" because he saw no prisms. The enamel

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has no prisms but is, in fact, "discontinuous". Fosse et al. (1985) found no organization of docodont enamel into prisms and interprismatic enamel, but rather, indications of "crystal clusters about 5 µm wide". Thus, Late Jurassic Docodonta preserve the conservative pseudoprismatic structure.

Eupantothere. Contemporaneously, however, partial prisms (boundaries) are present in the eupantothere in material from the same locality as the genus *Haldanodon*. Poole (1956, 1967) described prisms for an undetermined dryolestid by polarized light and Osborn and Hillman (1979) described "small arcs of prism sheaths" by polarized light in a dryolestid: their observations are confirmed and extended here with the resolution available through scanning electron microscopy.

Appearance of prisms and seams

Because of the significant gap in the fossil record between the Late Triassic and the Late Jurassic, we can determine neither the time when prisms were developed nor whether the second feature found in Eupantotheria, the seam, was developed before or at the same time as the prism. Perhaps the better question is whether the seam began to form at the same time as the rudimentary major planar discontinuity. It could be that the partial development of both coincides. In our suggested model (see below and Fig. 39) of the evolution of the secretory surface of the ameloblast, the seam was caused by a central ridge on the Tomes' process applied to the sloping floor-wall of the Tomes' process pit (Lester and Boyde, 1987). Given that the original cone-shaped Tomes' process was flattened and displaced at its apex, the ridge is then expanding the "one dimensional" convergence line and modifying it into a "two dimensional" seam. The angle of the flanks of this ridge would produce the difference in orientation of the crystallites: the steeper the ridge, the more pronounced would be the seam in the final enamel.

Within vertebrates, prismatic enamel has also been described in reptiles (Poole and Cooper, 1971; Cooper and Poole, 1973) and in multituberculates (Fosse et al., 1985; Carlson and Krause, 1985). Krause (1985) and Krause and Carlson (1986) have indicated the high degree of likelihood that fully prismatic enamel evolved in multituberculates independently of its evolution in other mammalian taxa. The Eupantotheria are regarded as having given rise to Eutheria and Marsupialia, in all three of which we observe the coexistence of prisms and seams. Prisms and seams are found together in the Late Cretaceous *Procerberus* (Lester, 1989b) and continue to exist together during the Tertiary and Quaternary in various mammalian groups. It seems that the development of the structural elements of enamel in terms of prism and seam took place during the Jurassic and Cretaceous. There followed an intensive development of the structural arrangement of these elements in the Tertiary and Quaternary (Koenigswald, Rensberger and Pfretzschner, 1987).

Changes in Tomes' Processes over Geological Time

In order to fully understand enamel adult structure in all its complex forms, it is essential to consider the underlying developmental processes involved. Boyde (1964; 1965; 1976; 1989) has written at length on the significance of the interface of the Tomes' processes with the mineralizing front and the effect of that morphology on the prism shape and the prism packing pattern ultimately expressed. It is possible to propose, in a preliminary way, an increase in the complexity of the developing front with geological time to account for the increase in complexity of adult enamel structure (see also Lester, 1988; 1989b; Carlson, 1989).

Simplistic, two dimensional representation of the contour of the developing (mineralizing) front required for these different levels of organization is shown in Figs. 39 and 40A. Obviously, within any one enamel, the differently structured layers necessitate change within the life cycle of the ameloblast at its secretory surface. We assume in the present account that all enamel domains are the products of hexagonally packed, columnar ameloblasts as the cells withdraw from the enameldentine junction. Thus, a flat surfaced cell, or Tomes' process, would produce continuous (aprismatic) enamel (Fig. 39a). The development of a Tomes' process with a simple conical shape, or a compressed conical shape, could account for the crystallite orientation described here in *Oligokyphus* and *Eozostrodon* - the crystallite orientation discontinuity feature would be a convergence line and relate to the tip of the Tomes' process (Fig. 39b). The lack of a completely regular and recurring pattern could be accounted for by relative differences in the degree of development of Tomes' processes at any one time. In *Haldanodon* enamel, the convergence line would be related to the tip of a more completely conical Tomes' process and, by extrapolation, the structural cell-based enamel "unit" would be equidimensional with ameloblast diameter (Fig. 39c). The partial prism outline of eupantothere enamel would require the development of a flat floor and a vertical wall to the Tomes' process pit; however partial that development might be in terms of the total circumference of the Tomes' process (Fig. 39d).

The basis for the alignment of the convergence lines of pseudoprismatic enamel with the mid-lines of prisms (and the seams) in prismatic enamel is illustrated diagrammatically in Fig. 40A. With regard to the remaining and more recent taxa examined in this study, the more complete the prism outline, the more the vertical wall of the Tomes' process would encroach on the total circumference of the Tomes' process. Where the seams were in conjunction with the necessarily incomplete prism outline, the sloping floor-wall of the pit would display the groove feature described in the bat, *Chalinolobus gouldii* (Lester and Boyde, 1987).

The generalised notion put forward here, of the complexity of the formative front and the completeness of the prism outline increasing with geological time (Fig. 39), lends itself ultimately to the view that circular prisms represent the more derived condition in mammals. Carlson and Krause (1986) have reviewed the literature on the primitive versus derived status of (circular prisms in) Pattern 1 enamel in mammals generally and, in a careful study of multituberculate enamel, concluded that circular prisms do not represent the primitive condition in multituberculates. Their work in multituberculates, and our observations reported here, are thus contrary to

the general proposals put forward by Sahni (1984, 1985), Kosawa (1984) and Boyde and Martin (1984) that complete, circular prisms in Pattern 1 arrangement represent the primitive condition in mammals.

Functional significance

In comparison to what is generally regarded as the prismless enamel of reptiles (with the exception of *Uromastyx*, see Poole and Cooper, 1971; Cooper and Poole, 1973), differentiation of enamel to show a convergence line, a seam or even a primitive prism should be of selective value. It is rather difficult at this stage to argue about the specific functional significance of the orientation of the crystallites but, in general, it seems to be more advantageous to possess crystallites oriented in different directions than oriented in parallel. It follows that the possibility of change in the secretory surface of the ameloblast to produce organized differences in crystallite orientation and modification of the enamel into differently structured layers (Figs. 39, 40) is of great importance. This ability leads to the formation of "true" prisms in later stages of evolution; the prisms being a significant factor in enhancing the stability of the enamel and preventing cracking (Koenigswald, 1988; Koenigswald and Pfretzschner, 1987). One can presume that any discontinuity of crystallite orientation leading eventually to the expression of prisms serves a similar, selectively advantageous purpose.

Nomeclature

There is a clear challenge here either to accept, modify or reject the terminology offered to describe the degree of development of features in enamel of the eupantothere. This enamel is clearly a meeting point of the pseudoprismatic (pre-prismatic) type with the prismatic type (Fig. 38); just as *Desmodus* is a meeting point of the prismatic with the post-prismatic. The enamel of *Ornithorhynchus* has previously been described as essentially post-prismatic (Lester and Boyde, 1986).

Sampling

We acknowledge that a limitation to exploring the internal structure of any tooth or tooth fragment by scanning electron microscopy is the difficulty involved with adequate sampling. The problem is often compounded with fossil material by the small size of the sample, uncertainty as to its relationship with the whole tooth, and quite reasonable restrictions that may be imposed by museum curators on destructive preparation. Even for teeth of extant mammals, major structures may occur in one part of the enamel and not in the other (as for the cuspal and cervical parts of *Desmodus*). The greatest likelihood of a repetitive pattern, if established, is in the thickest enamel, which is usually cuspal, and this may simply not be available for examination as was the case in this study with *Oligokyphus* and *Eozostrodon*. It goes without saying that finding a feature is more significant than not finding a feature where sampling is at all restricted. The thicker enamel of *Eozostrodon* samples as examined by others would appear to display a more ordered structure (for example, Osborn and Hillman, 1979; Grine et al., 1979).

Conceptual challenge

The future challenge is to accept and to accommodate in our thinking the rudimentary and partial prism and to be able to describe that enamel in terms of its discontinuities and significant domains. It is fortunate that the seam feature and the convergence line coexist to help subdivide the crystallite landscape. It is likely, and we are hopeful, that an expanded range of stages of the evolutionary life history of convergence line, seam and major planar discontinuity will be found with further study.

Conclusion

From these and other observations, we recognize the following structural features in the evolution of enamel ultrastructure: (i) a convergence line (minor linear discontinuity) related to the tip of the Tomes' process (more occasional and further apart in *Oligokyphus* and *Eozostrodon* and more regular in *Haldanodon*); (ii) a seam (minor planar discontinuity) related to the development of a central ridge on the Tomes' process and occurring in conjunction with (iii) a major planar discontinuity (where appropriate, prism boundary or prism sheath). This last may be so limited in extent as not adequately to enclose a domain (prism) and would be related to the partial development of a significant floor and wall angle to the Tomes' process pit (in the eupantothere). Where the major planar discontinuity is sufficiently extensive to enclose a recognizable domain (prism), it would be related to the fuller development of floor and walls of the Tomes' process pit (in *Amphiperatherium*, *Hassianycteris*, *Smilodon* and *Felis*).

The seam coexists with the development of the major planar discontinuity in the eupantothere, *Amphiperatherium*, *Hassianycteris*, *Smilodon* and *Felis*. Both features can be traced back to the Late Jurassic. For that time, the significant features are the minor discontinuities that both pre- and post-date the major planar discontinuity (and therefore the enamel prism) and, we suggest, offer a useful key in helping to unravel the natural evolutionary history of enamel.

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Discussion with Reviewers

D. Poole: Do the authors believe that the emergence of prismatic enamel during the evolutionary transition of mammals from reptiles is directly related to the coincident development of true mastication? If so, how does one account for the occasional appearance of prismatic enamel in reptiles?

Authors: As you imply, the proposal is clearly too simplistic in these terms. We look forward to further data collection and clarification of the complex relationship between phylogeny, ontogeny and function.

D. Poole: Tomes' processes are clearly the important factor in the differentiation of prisms and variation in prism character is a function of variations in Tomes' process shapes. Is the shape of the Tomes' process a genetically fixed character for a given species or is the shape at least partially influenced by other factors such as, perhaps, the crown morphology and the rate of production and thickness of enamel to be formed?

Authors: Clearly, the degree and rate of development (and regression) of the Tomes' process are fundamental to the expression of characteristic enamel form and, presumably, this expression is subject to a variety of intrinsic and extrinsic factors. It is known that although the Tomes' process pit is always much deeper in enamel which grows more rapidly, within any one tooth despite differences in rate of production, the depth of the pit does not change greatly. It is a complex question open to very much wider observation both at descriptive and experimental levels.

D. Poole: The mechanical "crack-stopping" advantage provided by the discontinuity of crystals at prism boundaries is discussed. Beyond this, aprismatic enamel with parallel crystals must be mechanically anisotropic whereas both crystal and prism divergence would render the enamel structurally isotropic with similar mechanical properties in all directions. Would this not also be of selective advantage in meeting the increased demands on teeth of mastication?

Authors: Although the proposal of a related selective advantage seems reasonable, we are unaware of examples of a derived enamel structure in which the mechanical properties are similar in different directions.

Reviewer IV: Can you state, succinctly, what heuristic benefit you ascribe to the terms "convergence line", "seams", and "major boundary plane"? In other words, how would you defend the charge that these terms further confuse rather than clarify our understanding of enamel ultrastructure?

Authors: "Convergence line" and "seam" are offered as everyday alternatives to the descriptive, definitive terms provided in the Introduction: "linear crystallite orientation discontinuity", and "minor planar crystallite orientation discontinuity", respectively. We prefer, for routine repetitive use, a total of 3 words to 9. The term "boundary plane" is not ours; it was introduced by Boyde in 1964 and continues to be extremely useful in the description of enamel ultrastructure.