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PROCERBERUS ENAMEL: A MISSING LINK

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Abstract

In a fossil tooth of *Procerberus* (a Late Cretaceous palaeoryctid insectivore), there is a unique, clear and simultaneous expression of all three known forms of enamel: prismatic, pseudoprismatic and aprismatic. The pseudoprismatic domain, generally regarded as the more primitive unit compared to the prismatic domain, may be interpreted in this material as that morphological territory in which the prism appears, or evolves, as an additional structural unit. It is possible to construct a three-dimensional, developmental scheme for *Procerberus* enamel on the basis of known principles and to use it to help build a conceptual bridge between synapsid and mammalian enamel.

KEY WORDS: Enamel evolution, prisms, pseudoprisms, seams, fossil insectivore, enamel development.

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Introduction

There has been a long-term challenge in the field of comparative dental histology: to marry within the one concept the three fundamental forms of mammalian enamel, prismatic, pseudoprismatic and aprismatic, taking into account considerations of both ontogeny and phylogeny (5, 6, 10, 12, 13, 18-20, 23, 25, 26). The different forms are expressed through different levels of continuity and discontinuity of the orientation of the component crystallite groups, there being already wide acceptance of the relationship between prismatic and aprismatic forms from a developmental point of view (2, 4, 7, 21, 22). The residual need is for interpretation of the pseudoprismatic form so as to bring it within the same unifying framework of developmental principles. In *Procerberus* (a Late Cretaceous palaeoryctid insectivore), a combined interpretation is greatly facilitated by the clear and simultaneous expression of all three forms of enamel in one fractured surface of the same tooth. Further, it is possible to explain and represent three-dimensionally the development of *Procerberus* enamel on the basis of known principles (1-4).

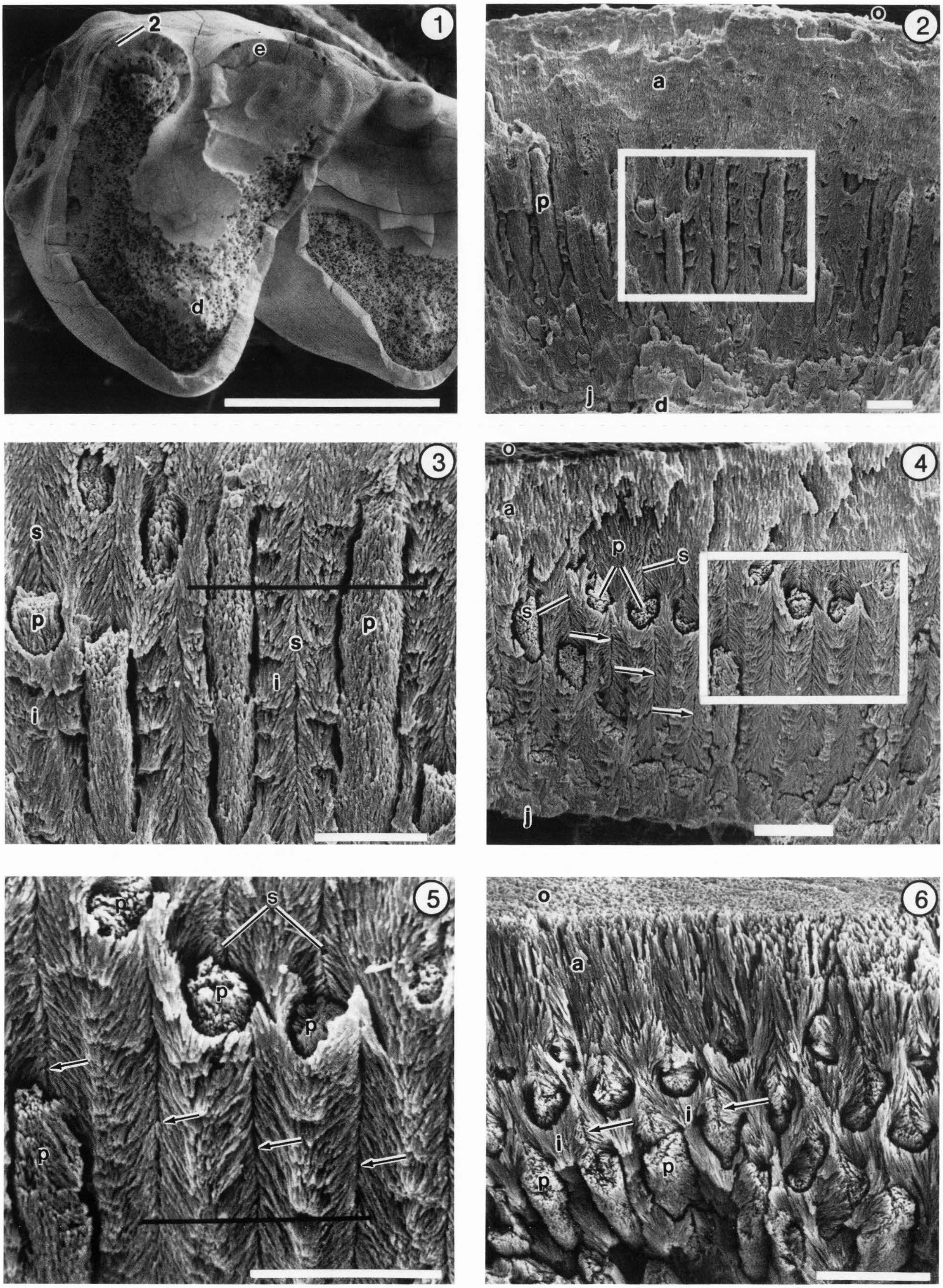
Materials and Methods

The naturally occurring (as found) occlusal surface (Fig. 1) of a lower third molar of *Procerberus* (a Late Cretaceous palaeoryctid insectivore - Bug Creek Anthills locality, Hell Creek Formation, Montana, U.S.A.) was air-polished™, etched with 1% H_3PO_4 for 5 sec, sputter-coated with gold and examined by scanning electron microscopy at 15 kV.

Results

The three expressions of enamel form exposed in the one fractured face of this specimen are (Figs. 1-6):

1. definitive prisms (ca. 3-4 µm diam.) demarcated by characteristic major boundary planes (4) and constituting repetitive, recognizable domains (Figs. 2-3);
2. definitive pseudoprisms (ca. 5-6 µm diam.) demarcated by minor boundary planes or seams (14, 15, 17) and constituting repetitive but larger recognizable domains within which the prisms reside (Figs. 4-5); and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3. definitive aprismatic enamel appearing as a substantial surface zone of parallel crystallite groups oriented perpendicular to the outer enamel surface and constituting a continuous, recognizable (non-prismatic, non-pseudoprismatic) domain (Figs. 2, 6).

←

Fig. 1. Survey view of naturally occurring (worn and fractured) occlusal surface of *Procerberus* molar. Numbered area indicates exposed enamel illustrated in Fig. 2 (e -enamel; d - dentine). Bar = 1 mm.

Fig. 2. Full thickness of enamel exposed in surface of *Procerberus* molar (see Fig. 1). From below: dentine (d); enamel-dentine junction (j); prismatic enamel (p); aprismatic enamel (a); and outer surface (o). The boxed area is magnified as Fig. 3. Bar = 10 µm.

Fig. 3. Enlargement of boxed area in Fig. 2. The enamel displays the following features: prisms (p); seams (s); and what would normally be regarded as "inter-prismatic" enamel (i) which structurally is in the form of an "extra-" or "peri-" prismatic honeycomb within which the prisms lie. The seams (s) are expressed where there is a convergence of crystallite groups towards the outer enamel surface (to top) in association with both the prisms and the "inter-prism". The black horizontal line is a reference plane for Fig. 10. Bar = 10 µm.

Fig. 4. Full thickness of enamel exposed in surface of *Procerberus* molar showing the relationship of prisms (p), pseudoprisms (between arrows) and seams (s). The boxed area is magnified as Fig. 5 (j - enamel-dentine junction; a - aprismatic enamel; o - outer enamel surface). Bar = 10 µm.

Fig. 5. Enlargement of boxed area in Fig. 4 showing longitudinal columns of fortuitously fractured out pseudoprismatic ("inter-prismatic", "peri-prismatic") enamel (between arrows); partially exposed prisms (p); and seams (s). Prior to enamel fracture, prisms would also have been in close association over the surface of the pseudoprismatic elements (see prism (p) at lower left) in conjunction with the seams (at arrows). The columns (between arrows) are an expression of the pseudoprismatic form of enamel found phylogenetically prior to the appearance of prisms and not normally recognizable in conjunction with prismatic enamel. The black horizontal line is a reference plane for Fig. 10. Bar = 10 µm.

Fig. 6. Obliquely fractured enamel towards the outer surface of the same specimen (Fig. 1) showing the relationship of seams (at arrows) to prisms (p) and what would normally be regarded as "inter-prism" (i). Note the transition from prismatic to aprismatic enamel (a) towards the outer surface (o). Bar = 10 µm.

Discussion

Developmental model

The theoretical relationship of the developing (mineralizing) surface to the formed enamel of *Procerberus* can be schematically represented in

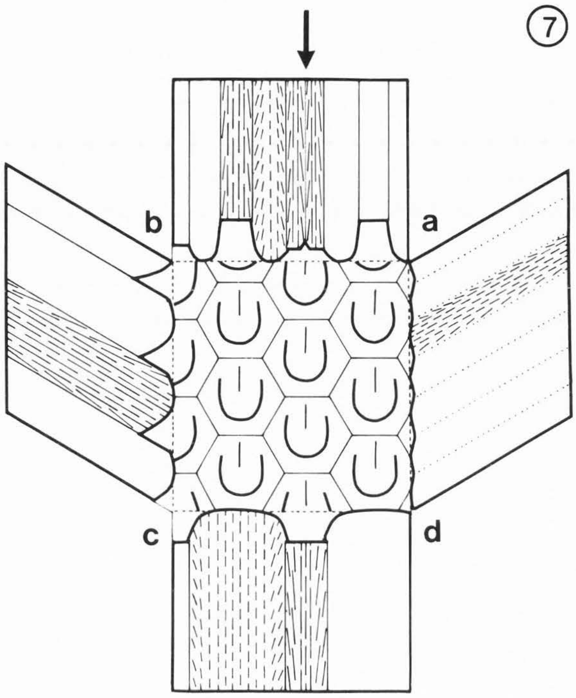

Fig. 7. Three-dimensional diagram of the proposed relationship between the developing (mineralizing) front and the formed enamel of *Procerberus* (based on drawings by Boyde (2, 4)). The drawing has been inverted from Boyde's original scheme to allow more direct comparison with Figs. 3-6.

The hexagonal outlines represent a plan view of the ameloblast cell borders at their junction with the Tomes' processes. The horse-shoes represent the junction of the vertical wall and flat floor of each of the Tomes' process pits in the developing enamel front. The four longitudinal faces arranged around the developing front represent sectioned formed enamel together with the corresponding section of the developing front at the section plane indicated (ab, bc, cd, da). The block can be "reconstructed" by folding along the dotted lines ab, bc, cd and da.

Section ab: produces part of two prisms: one with a seam running longitudinally (at arrow) and one without (at top left); between is the classical crystallite orientation of "inter-prismatic" (pseudoprismatic) enamel.

Section bc: produces longitudinal sections of prisms with no identifiable "inter-prismatic" (pseudoprismatic) enamel between.

Section cd: produces a prism without a seam (at right) and a large domain of "inter-prismatic" (pseudoprismatic) enamel (at left).

Section da: produces repetitive domains of "inter-prismatic" (pseudoprismatic) enamel with no prisms between.

three dimensions on the basis of known principles (1-4) (Fig. 7). This reconstruction is based on drawings by Boyde (1, 3) of two sides and a developing surface of a block of modern mammalian (Rhesus monkey, Pattern 2) enamel: the block could be "reconstructed" by an imagined folding back of the drawing along dotted lines at the edges of the developing surface so that the sides would meet at their common edges. From what is known of enamel development, the (derived) prismatic domain with its characteristic boundary discontinuity is, in essence, an expression of the development of a flat floor and a wall to the previously conical Tomes' process pit (see sectional faces ab, bc and cd in Fig. 7). The more fundamental (primitive) pseudoprismatic domain is, in essence, an expression of the cone-shaped bases of the Tomes' processes (see faces cd and da in Fig. 7). Fig. 8 is a two-dimensional diagrammatic representation of the changing configuration of the secretory surface (Tomes' process) of the ameloblast and therefore of the mineralizing front that could, in theory, account for the development of the three different forms of enamel where they occur in isolation. One could, however, anticipate a dynamic relationship between the various configurations of developing front from both a phylogenetic and an ontogenetic point of view - Carlson (5) has independently come to a similar conclusion.

Prism vs Pseudoprism

There is a conceptual and corresponding terminological difficulty which tends to obstruct our understanding in that we have, perhaps not unreasonably, come to accept the prism as the basic unit of mammalian enamel. This means that apart from the prism and its boundary (or "sheath"), all else is relegated to the somewhat lesser designation of "inter"-prism (interprismatic enamel or "substance") and rather ignored. In reality, this latter domain is the more primitive structural unit and is that morphological territory in which the prism appears or evolves as an additional structural unit. Further terminology in this already crowded area is unwelcome; nevertheless, this parent domain for the prism itself is more "extra-" or "peri-" than "inter-" prismatic. The three terms, however, focus on the ultimate unit denominator (prism) rather than the more elemental numerator (pseudoprism) and so none is entirely apt. The real point is that the pseudoprismatic form of enamel, characteristic of advanced synapsids, persists in mammals to coexist with the prismatic and the aprismatic: its designation as interprismatic and the fall from favor of the term pseudoprismatic (5, 20) have not helped our appreciation of this fact.

Enamel seam

Recognition of the enamel seam, minor boundary plane or additional crystallite discontinuity orientation factor (15, 17), as a further subdivision of the crystallite landscape is an important step in appreciating the two domains that co-exist in this particular specimen. The seam (Figs. 3-6) has been shown (14) to relate developmentally to a central groove in the mineralizing front (or obversely, a ridge on the cervical facing surface of the Tomes' process). In *Procerberus* enamel, the seam serves to accentuate and mark a border within the pseudoprismatic domain (Figs. 3-6).

Convergence line

It is important to remember that enamel, even when organized with discrete, complete boundary planes as in Pattern 1 prism packing, is a continuum (2) and that prisms, although a useful concept in the description of enamel structure, have no reality apart from their boundaries (9). The crystallite orientation discontinuity of the prism boundary (Fig. 8c) is the most extreme (or most derived) in the evolutionary history of enamel. It would seem that the least extreme (or most primitive) discontinuity is a convergence of crystallite tips on a linear "focus" which traces the withdrawal of the conical tip of the Tomes' process of the ameloblast (Figs. 8b and 9) through enamel during development: this could be termed a "convergence line" to distinguish it from the boundary planes (4) which develop at a later time in the history of enamel (16). It is likely that the appearance or expression of convergence line, seam and boundary plane as definitive features would have occurred over geological time so that enamels with different degrees of development of these three structural features will be found or recognized.

Pseudoprismatic domain

Fig. 9 is a three dimensional diagram of the hexagonal unit cell basis proposed for the development of pseudoprismatic enamel. The central "convergence lines" would each have related developmentally to the tip of a conical Tomes' process. The cut-away surfaces of the two cell-based "pseudoprismatic" units display the typical crystallite orientation of totally pseudoprismatic enamel (see also 5). The pseudoprismatic elements of *Procerberus* differ in so far as they do not occur in isolation (as in Fig. 9) but as part of a complex continuum in association with prisms and seams (Figs. 3-6).

Exposure of the discrete longitudinal columns representing pseudoprismatic domains in *Procerberus* (Fig. 5) would have resulted from a fracture plane that could be envisaged as passing diagonally with a scalloped outline across the proposed reconstructed developing front so as to avoid the horseshoe prism boundaries but strike the seams (Fig. 10). These fortuitously exposed pseudoprismatic domains represent, in isolation at this surface (cf. Fig. 9) , the structural analogues of: the "cylindrical groups of crystallites" previously described by polarized light microscopy in synapsid reptiles (23); the "hexagonal columns" previously deduced, also by polarized light microscopy, in cynodonts and *Eozostrodon* (20); and the "pre-prismatic" and "pinnate" patterns devoid of "interprismatic material" described by scanning electron microscopy in *Haramiya* (10) and *Kuehneotherium* (26). A totally pseudoprismatic enamel form could also possibly account for the structure assessed as "prismatic" in a heavily etched specimen of *Eozostrodon* by scanning electron microscopy (12). Another missing link might be a pseudoprismatic enamel with seams and without prisms: perhaps if found, it would not be too dissimilar to the enamel of placodont reptiles (25) or to the (already described but heavily etched) enamel of *Pachygenelus* (11). Accounts of the possible evolutionary relationships of the taxa mentioned above are available elsewhere (8, 24).

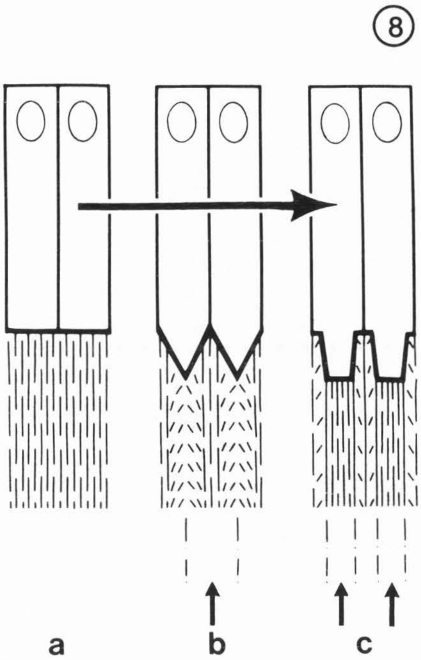

Fig. 8. Two-dimensional diagram of the changing morphology of the basal ends (Tomes' processes) of ameloblasts which, it is proposed, could account for the production of: (a) aprismatic enamel; (b) pseudoprismatic enamel; and (c) prismatic enamel. The increase in complexity of the Tomes' process, and therefore of the mineralizing front, which would occur over geological time (large arrow), would result in an increasing structural complexity of formed enamel. Small arrows indicate, between the broken lines, a "pseudoprism" in (b) and prisms in (c).

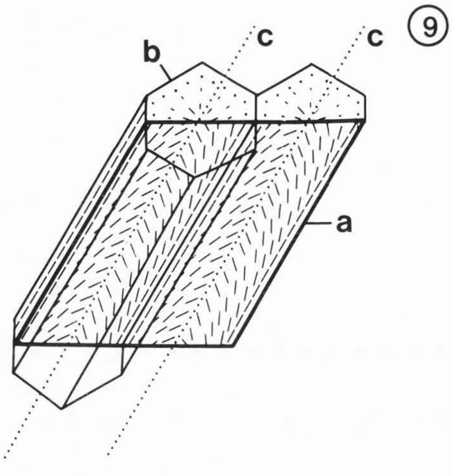

Fig. 9. Three-dimensional diagram relating crystallite orientation in totally pseudoprismatic enamel (bold outline (a) represents longitudinal cut-away section) to the hexagonal ameloblast cell outline (b). The centrally placed convergence lines (extended at c) would each have related developmentally to the centrally placed tip of a conical Tomes' process. Note that the true cell-based pseudoprismatic unit has parallel crystallites at its three-dimensional periphery and the linear discontinuity in crystallite orientation (convergence line) at its centre.

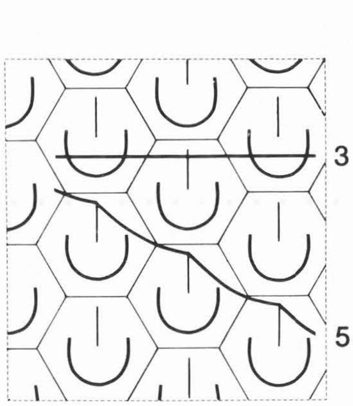

Fig. 10. Interpretation of fracture planes (3 and 5) relative to the reconstructed developing front (see Fig. 7) necessary to produce the longitudinal and longitudinal/oblique fields in Figs. 3 and 5 respectively. The prism boundaries have been shortened compared to those in Fig. 7 in order to compensate for the artificial perpendicularity of the prism axis alignment depicted in this scheme compared to the actual specimen.

Conclusion

Clearly defined prismatic, pseudoprismatic and aprismatic enamel coexist in conjunction with enamel seams in the 65 million year old eutherian *Procerberus*. It is anticipated that this structural account and accompanying developmental interpretation will help in the analysis of other fossils and so smooth the conceptual path between the aprismatic, pseudoprismatic and prismatic forms which, in various degrees of development and in various combinations, constitute the intricate evolutionary continuum of enamel.

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References

1. Boyde A. (1976). Amelogenesis and the structure of enamel. Scientific Foundations of Dentistry. (eds) Cohen B, Kramer IRH. William Heineman Medical Books Ltd, London. Chapter 27, pp.335-352.

2. Boyde A. (1967). The development of enamel structure. Proc R Soc Med. 60, 923-928.

3. Boyde A. (1965). The structure of developing mammalian dental enamel. Tooth Enamel. (eds) Stack MV, Fearnhead RW. John Wright & Sons, Bristol. pp.163-167.

4. Boyde A. (1964). The structure and development of mammalian enamel. PhD Thesis, University of London.

5. Carlson SJ. (1989). Vertebrate Dental Structures. Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. (ed) Carter JG. American Geophysical Union, Washington, D.C. In press.

6. Carlson SJ, Bartels WS. (1986). Ultrastructural complexity in reptilian tooth enamel. Geo Soc Amer, Abst with Programs 18:558.

7. Cooper JS, Poole DFG. (1973). The dentition and dental tissues of the agamid lizard, *Uromastyx*. J Zool. 169, 85-100.

8. Crompton AW, Jenkins FA. (1979). Origin of Mammals. Mesozoic Mammals. The First Two-Thirds of Mammalian History. (eds) Lillegraven JA, Kielan-Jaworowska Z, Clemens WA. Uni of California Press, Berkeley, CA. Chapter 3. pp.59-73.

9. Fortelius M. (1985). Ungulate cheek teeth: developmental, functional and evolutionary interrelations. Acta Zool Fennica. 180, 1-76.

10. Frank RM, Sigogneau-Russell D, Voegel JC. (1984). Tooth ultrastructure of Late Triassic Haramiyidae. J Dent Res. 63, 661-664.

11. Grine FE, Vrba SE. (1980). Prismatic enamel: a pre-adaption for mammalian diphyodonty. S Afr J Sci. 76, 139-141.

12. Grine FE, Vrba ES, Cruickshank ARI. (1979). Enamel prisms and diphyodonty: linked apomorphies of Mammalia. S Afr J Sci. 75, 114-120.

13. Ishiyama M. (1987). Enamel structure in Odontocete whales. Scanning Microsc. 1, 1071-1079.

14. Lester KS, Boyde A. (1987). Relating developing surface to adult ultrastructure in chiropteran enamel by SEM. Adv Dent Res. 1, 181-190.

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

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

17. Lester KS, Hand SJ, Vincent F. (1987). Adult phyllostomid (bat) enamel by scanning electron microscopy - with a note on dermopteran enamel. Scanning Microsc. 2, 371-383.

18. Moss ML. (1969). Evolution of mammalian dental enamel. Amer Museum Novitates 2360, 1-39.

19. Moss ML, Kermack KA. (1967). Enamel structure in two Triassic mammals. J Dent Res. 46, 745-747.

20. Osborn JW, Hillman J. (1979). Enamel structure in some therapsids and Mesozoic mammals. Calcif Tissue Int. 29, 47-61.

21. Poole DFG. (1967). Phylogeny of tooth tissues: enameloid and enamel in recent vertebrates, with a note on the history of cementum. Structural and Chemical Organization of Teeth. (ed) Miles AEW. Academic Press, New York. Chapter 3, pp.111-149.

22. Poole DFG. (1962). Odontogeny of enamel structure. J Bone Jt Surg. 44B, 959.

23. Poole DFG. (1956). The structure of the teeth of some mammal-like reptiles. Q J Micro Sci. 97, 303-312.

24. Rowe T. (1988). Definitions, diagnosis and origin of Mammalia. J Vertebrate Paleontology 8/3, 241-264.

25. Schmidt WJ, Keil A. (1971). Polarisation Microscopy of Dental Tissues. Pergamon Press, Oxford. Chapter 3, pp.319-459.

26. Sigogneau-Russell D, Frank RM, Hemmerle J. (1984). Enamel and dentine ultrastructure in the Early Jurassic therian *Kuehneotherium*. Zool J Linn Soc. 82, 207-215.

Editor's Note: All of the reviewer's concerns were appropriately addressed by text changes, hence there is no Discussion with Reviewers.