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ENAMEL OF YALKAPARIDON COHENI: REPRESENTATIVE OF A DISTINCTIVE ORDER OF TERTIARY ZALAMBDODONT MARSUPIALS

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Abstract

The enamel of an incisor and a premolar of Yalkaparidon coheni was examined by scanning electron microscopy in fractured and in sectioned, polished surfaces. The enamel of both teeth demonstrated: complete, ovoid and horse-shoe shaped prisms in a Pattern 2 arrangement; a simple parallel prism course; and, enamel tubules in abundance in the premolar but restricted to the innermost enamel in the incisor. Overall, the enamel ultrastructure supports the marsupial affiliation proposed for Yalkaparidon coheni but does not unambiguously ally it with any other order of marsupials.

The observation of a significant ultrastructural difference between the anterior and posterior teeth of a marsupial emphasizes the need to sample both if available. In pursuing this, we report here also the lack of tubules in the anterior teeth of the extant Tarsipes rostratus. This together with a similar absence of typical marsupial tubules from the incisor of the extinct Yalkaparidon coheni, would suggest that the wombat is not the only surviving marsupial to have experimented so extensively with this particular structural feature. It is likely that further study will demonstrate an unexpected and relative lack of tubules in the incisor enamel of other fossil Australian marsupials.

KEY WORDS: enamel ultrastructure, fossil marsupial, taxonomy, prism pattern, enamel tubules.

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Introduction

Newly discovered, as yet unnamed fossiliferous deposits in northwestern Queensland have led to the recovery of more than 200 new species of Tertiary vertebrates. Of these, Archer et al. (1988b) have recently described Yalkaparidon coheni and Yalkaparidon jonesii as representing the first fossil record of a new order (Yalkaparidontia) of Australian zalambdodont marsupials (for a consideration of zalambdodonty with particular reference to Australian marsupials, see Archer (1984)). On the basis of current palaeoecological interpretation, these Riversleigh zalambdodonts represent rainforest species (Archer et al., 1988a). The phylogenetic interpretation was based on examination of the gross morphology of the skull and teeth. Because enamel histology and ultrastructure is becoming increasingly accepted as a useful taxonomic indicator (e.g., Shobusawa, 1952; Boyde and Martin, 1984; Krause and Carlson, 1986, 1987; Lester et al., 1987a,b), the enamel of two teeth of Yalkaparidon coheni was sampled by scanning electron microscopy to assist its characterization and comparison with other known marsupial enamels.

Materials and Methods

The teeth of Yalkaparidon coheni involved in this study, an isolated incisor and a premolar, exhibit the highly distinctive morphology seen in other complete specimens from the same locality (Archer et al., 1988b). The teeth were collected from newly discovered and unnamed late Oligocene to middle Miocene limestone deposits on Riversleigh Station, northwestern Queensland, having been prepared initially by emersion of the surrounding limestone in dilute acetic acid and subsequent washing in tap water (Archer et al., 1988b).

The lower incisor, as received for scanning electron microscope examination, had only limited, exposed, inner surfaces available for examination. Because of the rarity of the specimen, it was first attached to the specimen stub by conductive putty alone and examined without any preparation in a JEOL 840 ("JEOL" Ltd., Tokyo, Japan) scanning electron microscope (SEM) at low kV. The enamel surfaces available were then progressively modified in order to clean them and expose

intrinsic detail. The preparation modes and kilovoltage at which the specimen was examined were: (i) as obtained without coating at 5 kV; (ii) after sputter-coating with gold at 15 kV; (iii) after airpolishing ("Prophy-Jet", Dentsply International Inc., York, PA.) (Boyde, 1984) and coating at 15 kV; and (iv) after airpolishing, etching with 2.5% H_3PO_4 for 18 secs. and coating at 15 kV. The incisor was then embedded in Spurr's resin and sectioned first transverse to and then parallel with the longitudinal axis of the tooth. The surfaces were polished and etched (1% H_3PO_4 for 10 secs.) and coated prior to examination in the SEM.

The premolar, being intact, was examined on its external aspect and then fractured longitudinally to expose an internal surface of enamel. This surface was progressively air polished, etched, coated and examined in the SEM. The premolar specimen was then embedded in Spurr's resin and sectioned transverse to the longitudinal axis of the tooth. The surfaces were polished and etched (1% H_3PO_4 for 10 secs.) and coated prior to examination in the SEM.

Stereopair images at a tilt angle of 10° were taken where appropriate.

Results

Incisor

Fractured surfaces. Observations resulting from the preparation modes (i) - (iii) for the fractured surface were subsequently confirmed and superseded, in terms of clarity of ultrastructural detail, by mode (iv). As anticipated, much accumulated debris was removed from the surface by the airpolishing; the detail of prisms and of crystallite orientation was highlighted by the etching; and coating and increasing the kilovoltage resulted, as would be expected, in a more satisfactory SEM image.

The specimen as examined in the SEM was essentially the result of a fortuitous longitudinal fracture exposing pulp chamber, enamel and dentine to reveal the generalized form of a continuously forming and growing (rodent-like) incisor (Fig. 1). A transverse exposed edge of enamel, at what was interpreted as the apical end of the specimen (because of the greater size of the pulp chamber and lesser thicknesses of enamel and dentine), presented many differently angled facets which, together with the subsequent viewing of stereopair images (Fig. 2), provided a satisfactory composite picture of the enamel.

i) Prism course: In the thickest part of the enamel as seen in the transverse plane, the prisms initially run a straight course angled away from the mid-line at approximately 30° to the enamel-dentine junction (Figs. 2, 3). The prisms undergo a gentle undulation approximately one-third of their way to the outer enamel surface and again at about two-thirds of the way (Fig. 3) - also see below for sectioned specimen (Fig. 8). As a result, the prisms in transverse section appear stacked more or less parallel with the enamel-dentine junction in the innermost part of the enamel and perpendicular to it in the outermost part (Fig. 4). Similarly, the inter-row sheets are parallel to the junction in the inner part, angled in the middle part and perpendicular to it in the outer part of the enamel (Figs. 2, 4). The prisms are remarkably parallel at all times and are themselves separated within each column by inter-prismatic leaves (Fig. 5). In the thinner, more lateral enamel away from the longitudinal mid-line of the specimen, the prisms undertake a single bend only in the mid-point of the enamel to run in an incisal direction (Fig. 6).

ii) Prism shape and size: The prisms are complete at all times and are generally ovoid in the outer enamel (Fig. 3) and horse-shoe shaped in the inner enamel with, in the latter case, the convexity on the aspect away from the enamel-dentine junction (Fig. 5). There is little variation in maximum prism transverse diameter (ca. 3.3 µm).

iii) Prism packing pattern: The prism packing is distinctly Pattern 2 (after Boyde, 1964, 1965) (Figs. 4-6). As described above, the packing is not always in the same direction, there being generalized areas of horizontal packing (inner enamel) and vertical packing (outer enamel) relative to the enamel-dentine junction (Figs. 2, 4 and see sectioned enamel Fig. 10 below). The packing pattern, relying as it does on a number of factors including prism shape, prominence of inter-row sheet and inter-prism component, fits readily into the Pattern 2 category because of the dominance of the inter-row sheet, which increases progressively towards the outer enamel surface (Fig. 3).

iv) Tubules: There is no evidence of tubules as a

Figs. 1 - 15 are scanning electron micrographs of prepared surfaces of teeth of Yalkaparidon coheni.

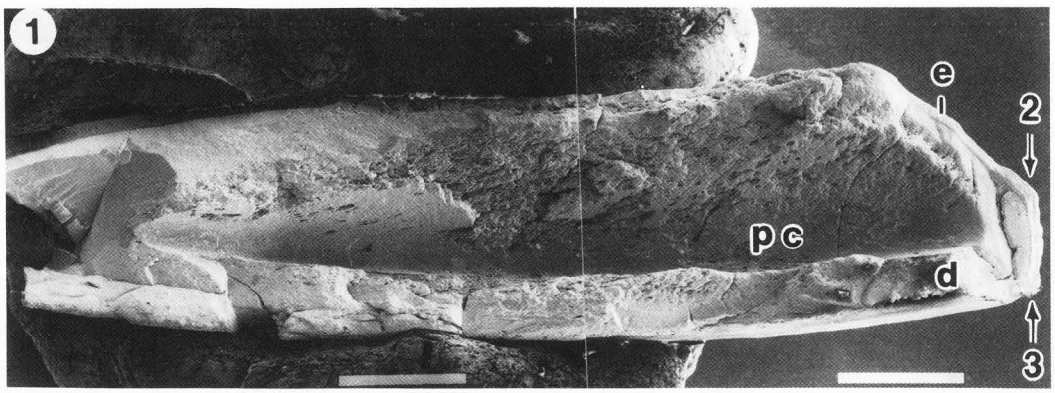
Figs. 1 to 7 are of fractured etched surfaces of incisor enamel.

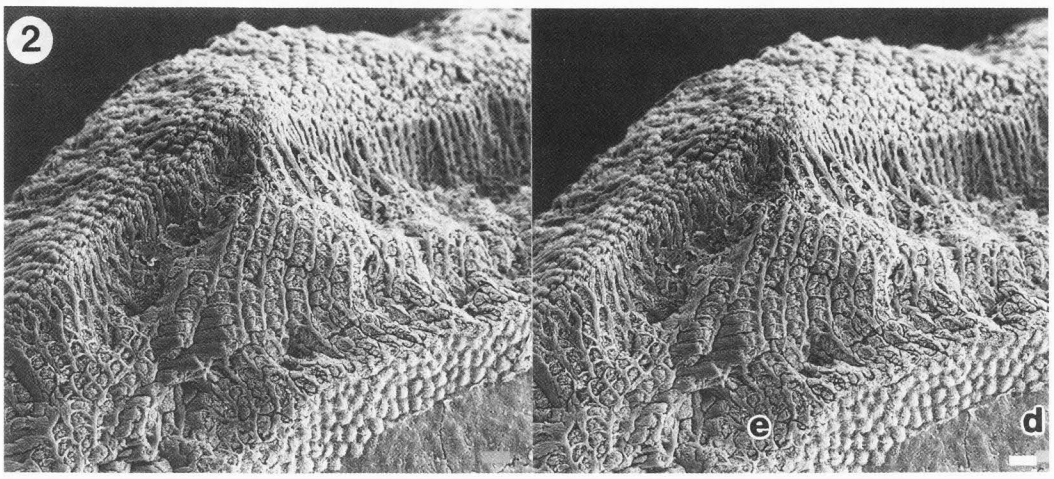
Fig. 1. The pulp chamber (pc) lies centrally surrounded by dentine (d) and enamel (e). The fractured surface examined extensively is at the right-hand end: the exposed enamel is localized by arrows for Figs. 2 and 3. Bar = 1 mm.

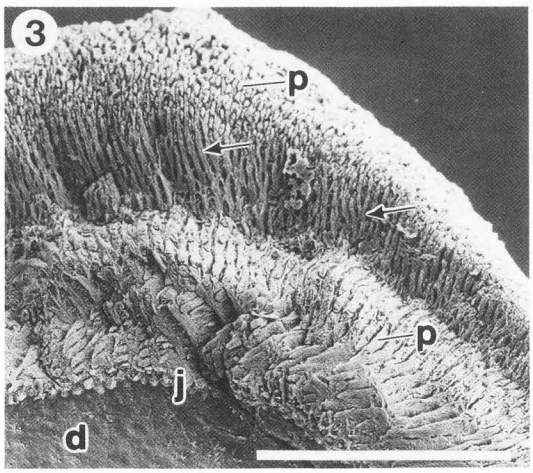
Fig. 2. Stereopair of fractured enamel surface (e) showing a partial thickness of the enamel (outermost enamel lost at top left). The dentine (d) is at right below a tangential fracture through the enamel-dentine junction displaying the bases of the prisms. The horizontal, angled and vertical stacking of the prisms is evident in this surface (see Fig. 1 for location). Bar = 10 µm.

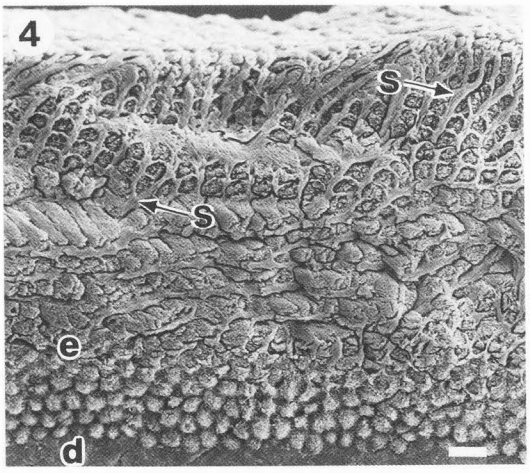
Fig. 3. The prisms (p) are angled to the enamel-dentine junction (j) and undulate twice on their way to the outer surface. Note that the prisms dominate the inner half of the enamel and the inter-row sheets (at arrows) dominate the outer half of the enamel (see Fig. 1 for location). Bar = 100 µm.

Fig. 4. The Pattern 2 arrangement of the prisms is clear with the horizontal, angled and vertical stacking of prisms. Note the branching of the inter-row sheets (s) in (at arrows) the outer part of the enamel (e) and the appearance of inter-prismatic "leaves" (see also Fig. 6). Bar = 10 µm.









common characteristic of the incisor enamel in fractured surfaces. This is borne out with the fortuitous exposure of the inner (dentinal) bases of the prisms at the artificially eroded enamel-dentine junction where there is only the suggestion of occasional tubules (Figs. 2, 7). There is an accompanying lack of patent dentinal tubules immediately beneath the enamel (Figs. 2-4) in what would be the von Korff's fibre dentine (see Lester and Boyde, 1968).

v) Crystallite orientation: There is a characteristic and preferred orientation of crystallite

LEGENDS TO ILLUSTRATIONS

Abbreviations

c - cusp
d - dentine
e - enamel
i - inter-prism
j - enamel-dentine junction
o - outer enamel surface
p - prism
pc - pulp chamber
s - inter-row sheet
t - tubule

groups in the longitudinal axis of the prisms (Figs. 5-6). Inter-row and inter-prismatic crystallite groups are parallel with each other and always at a distinct (up to 90°) angle to those of the prisms. This difference in angle lessens dramatically at the outer enamel surface. The outermost layer of enamel, where intact, is very thin and non-prismatic, the parallel crystallite groups being oriented generally perpendicular to the profile of the outer enamel surface (Fig. 6).

Sectioned surfaces. The embedded specimen confirmed, through the advantageous flat surfaces prepared, the parallelism of the prisms and the undulations in their course from enamel-dentine junction to outer enamel surface (Fig. 8). Most importantly, the presence of a small number of tubules was confirmed in the innermost enamel near and at the enamel-dentine junction (Fig. 9) as was the lack of tubules in the greater and remaining bulk of the enamel. Complete, horse-shoe shaped prisms were stacked vertically in a classic Pattern 2 arrangement (Fig. 10).

Premolar

The longitudinally fractured enamel surface of the premolar also exhibited long, essentially parallel prisms angled towards the tooth cusp from the enamel-dentine junction and curving again very slightly in the outer one third of their length towards the cuspal tip (Fig. 11). Enamel tubules were abundant in the fractured premolar enamel (Fig. 12) unlike the incisor specimen, and occurred characteristically at the interface between prism and inter-row sheet (Fig. 13); the proximity of large diameter dentinal tubules to the enamel-dentine junction confirmed their identification. Pattern 2 prism stacking was evident particularly in the outer enamel where the inter-row sheets came to dominate the prisms (Fig. 14).

Discussion

The incisor and premolar enamel of Yalkaparidon coheni is characterized by three major features: (i) horse-shoe shaped prisms (av. diam. 3.3 µm) in the inner enamel, which become ovoid and flattened in the outer enamel and which are packed in a Pattern 2 arrangement (after Boyde, 1964, 1965)) with a very pronounced inter-row sheet developing to dominate the outer half of the enamel thickness; (ii) a simplicity and parallelism of prism course, with an incisal or cuspal bend of prisms in the outer third of both teeth and with regular minor undulations in the inner two thirds of the thickest enamel of the incisor; and, (iii) a relative absence of tubules in the incisor except in the innermost enamel close to the enamel-dentine junction and an abundant presence of tubules in the enamel of the premolar. The possible phylogenetic significance of each of these major characteristics should be considered in depth when more detailed information on Australian marsupials is available. For now, we can only comment in very general terms.

Prism shape and packing

Pattern 2 enamel is recognised as one of three main types based on a combination of prism cross-sectional shape and prism packing pattern (Fig. 15) (Boyde, 1964, 1965). Pattern 2 enamel is a common and distinct entity and represents movement of the ameloblasts relative to the developing front along rows resulting, in the adult structure, in close-packed, horse-shoe shaped prisms in longitudinal arrays organized predominantly in an occluso-cervical direction separated by inter-row sheets. The pattern is found in perissodactyls, artiodoctyls, marsupials, lagomorphs,in limited areas of human and monkey enamel and in a much modified form in rodents (Boyde, 1964; Boyde and Martin, 1984). For marsupials, Beier (1984) has further divided eight families into two groups based on the relative amount of "inter-prismatic enamel" about individual prisms, although there is little doubt that the prisms remain in rows in both groups. It is well to bear in mind, however, as pointed out by Fortelius (1985) that although prisms are a

Fig. 5. Higher magnification of part of Fig. 4 to show the orientation of the crystallites: in the preferred axis of the prisms (p); at right-angles to the predominant crystallite orientation in the prisms in the inter-row sheet; and at right-angles to both in the inter-prismatic leaves of crystallites (i) separating the prisms in their vertical stacking. Bar = 10 µm.

Fig. 6. A full thickness of lateral (thinner) enamel. Note the single bend in the prisms (p) as they pass from the enamel-dentine junction (at right) to outer enamel surface (o at left). Note also the dominating inter-row sheet (s) of the Pattern 2 arrangement and the very thin prismless outer enamel (at top left) where the crystallites are perpendicular to the outer enamel surface. Bar = 10 µm.

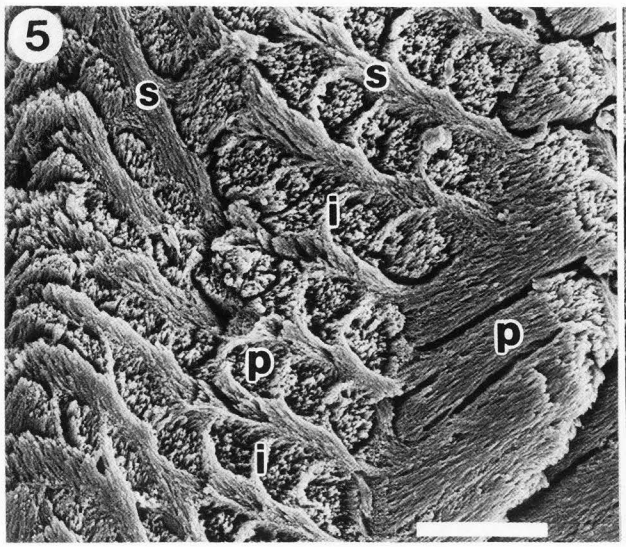
Fig.7. Higher magnification view of part of Fig. 2 to show the lack of patent tubules in the dentine (d) and the very few and isolated (possible) tubule openings in the individual bases of the prisms (at arrows) in the enamel (e). It would be very difficult definitively to identify this as a tubular enamel from this evidence alone. Bar = 10 µm.

Figs. 8 to 10 are of polished, etched surfaces of incisor enamel.

Fig. 8. Shows the two undulations (at arrows) in the course of the prisms from the enamel-dentine junction (towards the lower left) on their way to the outer enamel surface (at top right). Bar = 10 µm.

Fig. 9. The enamel-dentine junction (j) showing isolated tubule openings in the dentine and definitive enamel tubules (t) in the very first part of the innermost enamel (e). Positive enamel tubule identification can be made here. Bar = 10 µm.

Fig. 10. This area shows clearly the Pattern 2 prism packing: complete horse-shoe shaped prisms (p) in vertical stacks separated by inter-row sheet (s). Bar = 10 µm.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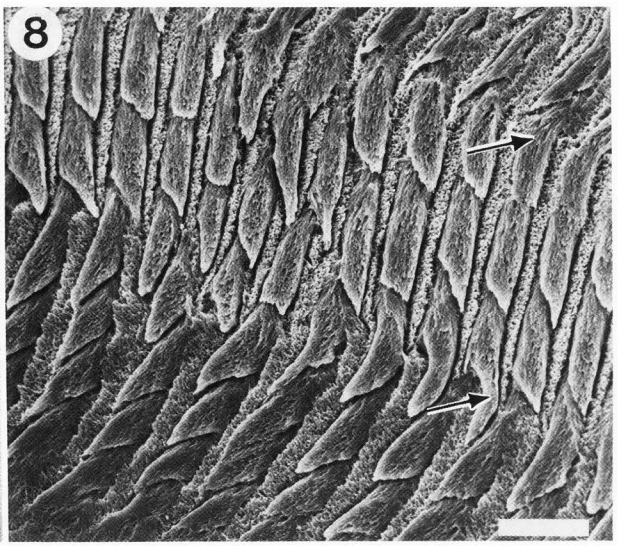
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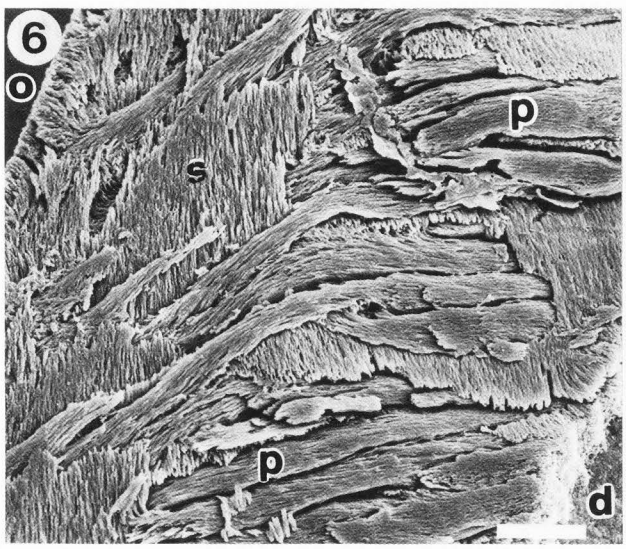
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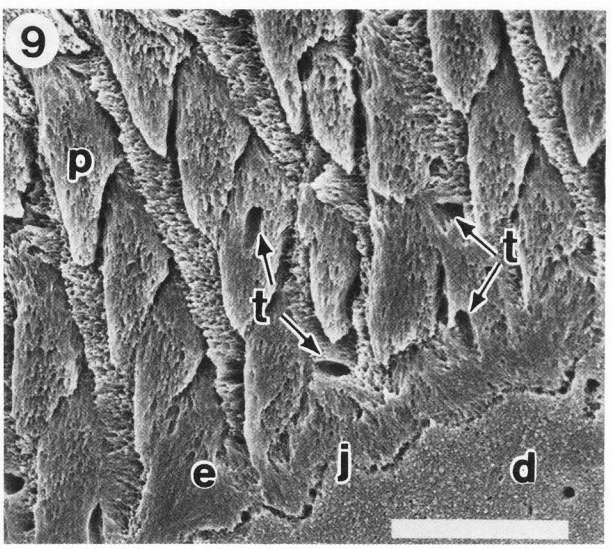
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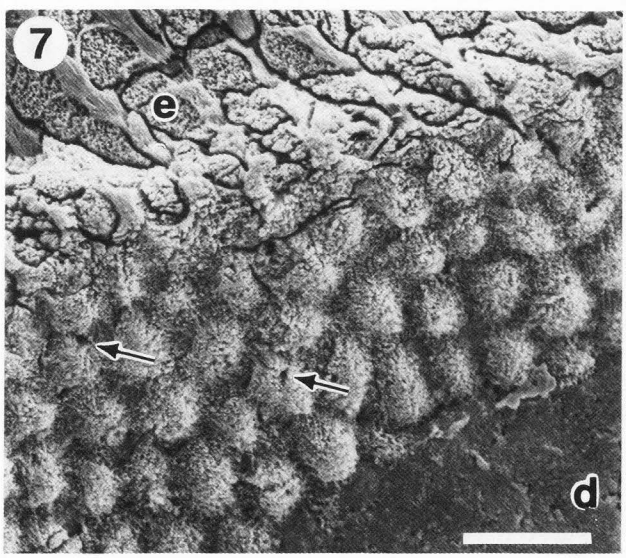
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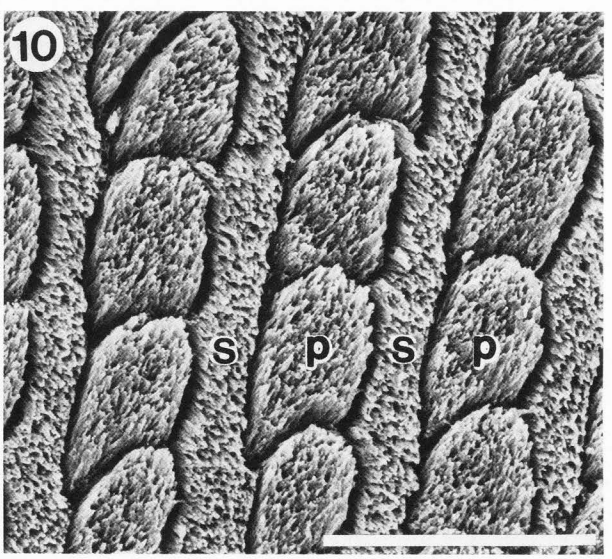
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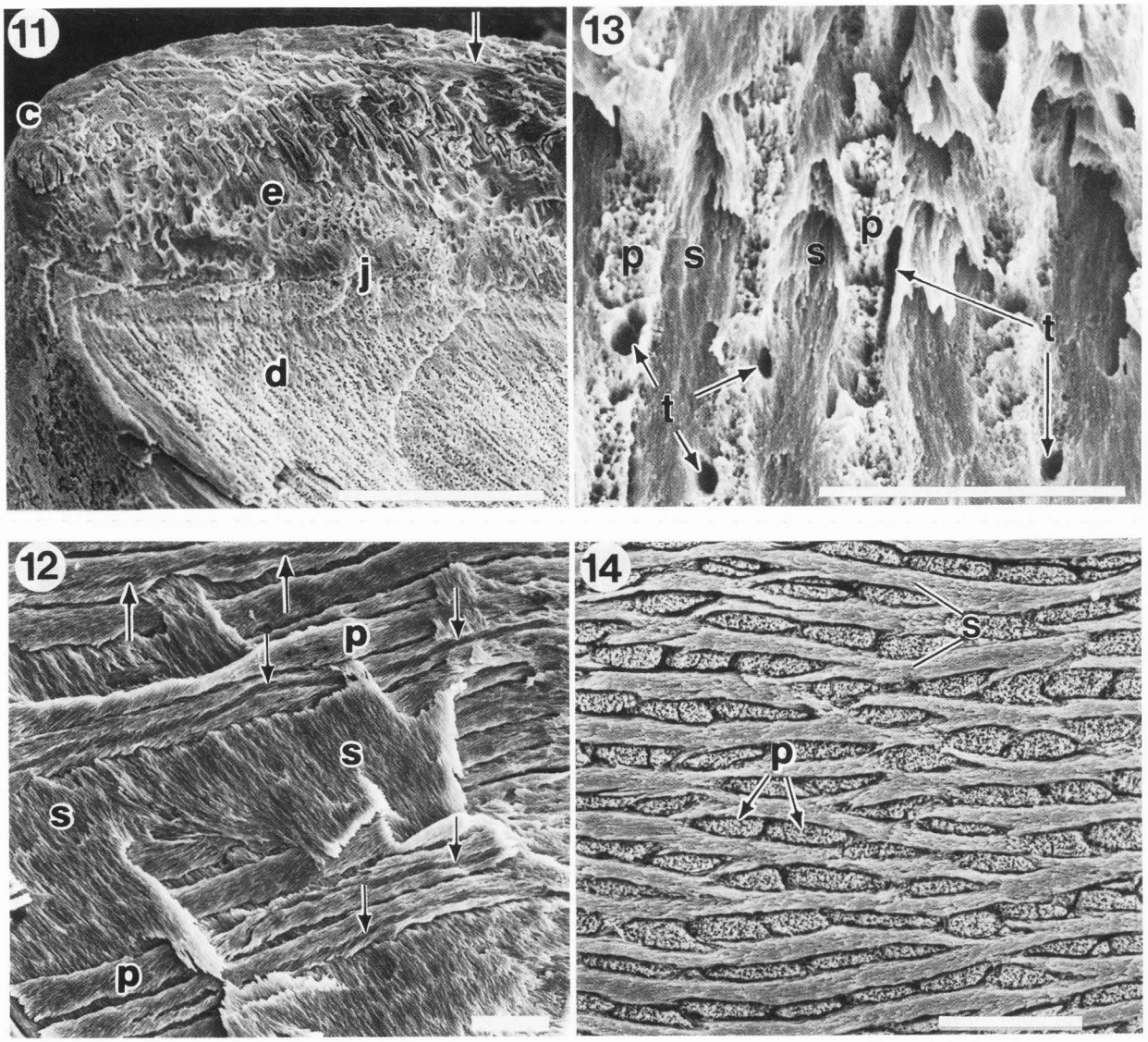


Figs. 11 to 14 are of fractured etched surfaces of premolar enamel.

Fig. 11. Shows the full thickness of the enamel cusp (c) to left and the dentine (d) to lower right. The prisms take a simple course from the enamel-dentine junction (j) to the outer enamel surface bending slightly in their outermost part towards the cusp. Circumferential incremental lines are evident (at arrow) in the outer enamel and there is already a clear impression of a strong inter-row sheet (see Fig. 12). Bar = 100 µm.

Fig. 12. Higher magnification of part of Fig. 11 confirms the Pattern 2 arrangement and clearly identifies numerous tubules (at arrows) running within the prisms. Inter-row sheet is at s. Bar = 10 µm.

Fig. 13. Higher magnification of stacked (but difficult to identify) transversely sectioned prisms (p) between inter-row sheets (s). Numerous transversely and obliquely sectioned tubules (t) are shown clearly in association with the poorly defined prism outlines. Bar = 10 µm.

Fig. 14. A polished etched surface of the outer part of premolar enamel showing the Pattern 2 packing of ovoid prisms (p) with a very strong and dominating inter-row sheet component (s). Bar = 10 µm.

Fig. 15. Diagram showing prism patterns or cross-sectional outlines of the prism boundaries or "prism sheaths". The lines represent planes of abrupt change in crystallite orientation within the enamel. A: Pattern 1; predominant in members of the Orders Cetacea (Odontoceti), Insectivora and Sirenia (Chiroptera previously included). B: Pattern 2; Ungulata and Marsupialia, also in Primates. C: Pattern 3; Primates, Proboscidea, and Carnivora. D: Murine incisor inner enamel (Boyde, 1964).

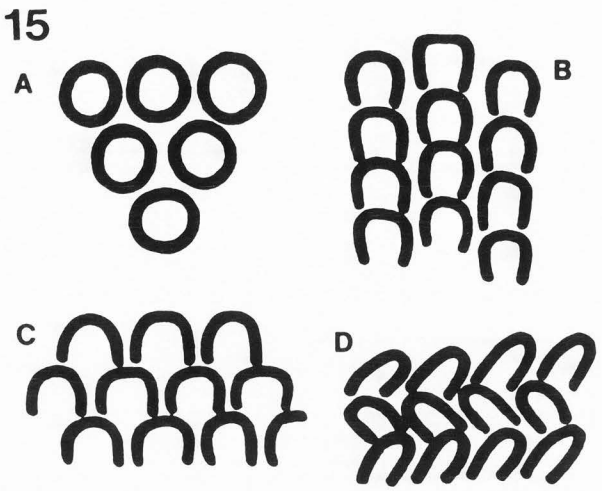


Fig. 16. A polished etched surface of the enamel of a molar of Tarsipes rostratus with the enamel-dentine junction to the right-hand side. The prisms (p) are complete in a Pattern 1 arrangement and there is evidence of two tubules (at arrows) each in the middle of a prism to the right-hand side (which is the aspect towards the enamel-dentine junction). Bar = 10 µm.

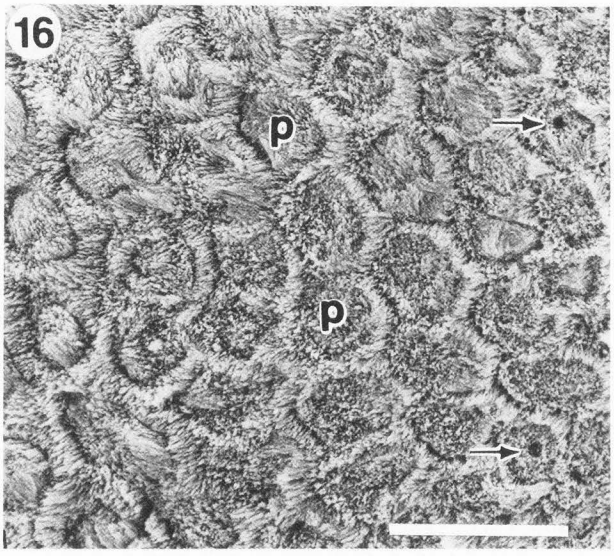
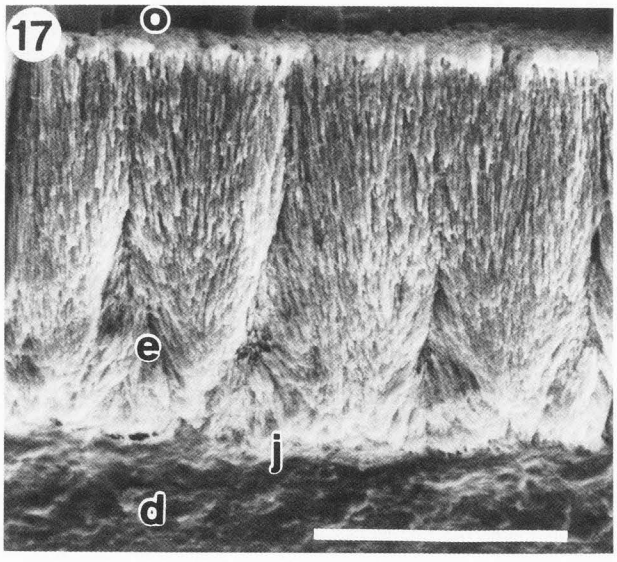


Fig. 17. A polished etched surface of the enamel (e) of a lower incisor of Tarsipes rostratus showing "columns" of crystallites radiating from the enamel-dentine junction (j) to outer enamel surface (o). This very thin enamel does not form recognisable prisms nor is there any evidence of tubules. Bar = 10 µm



useful concept in the description of enamel structure, they have no reality apart from their boundary discontinuity. Further, there are occasionally indeterminate areas within any one pattern and graduations between the three patterns - see also Lester and Hand (1987) in their description of chiropteran enamel.

Prism course

Although the prisms at all times are remarkably parallel to one another, the undulations in prism course represented in the differently angled facets of the fractured surface of the incisor enamel appeared superficially to represent parazones and diazones and certainly confused our initial interpretation; that is to say, before the surface was progressively and adequately cleaned. These sudden changes expressed in the facets of the fractured surface, combined with the predominance and coherence of the inter-row sheets, give the specimen at first acquaintance the appearance of a serial enamel (Korvenkontio, 1934-35; Wahlert, 1968; Sahni 1980, 1984; von Koenigswald, 1985). This impression was particularly convincing in the outer third enamel of the fractured incisor specimen where the inter-row sheets are arranged radially and parallel each other in a direction perpendicular to the outer enamel surface (Fig. 3). This possible confusion to the unwary observer of strong parallel inter-row sheets in Pattern 2 enamel with prism decussation is not new (see Boyde, 1969). That these are inter-row sheets in this particular enamel is confirmed by their being seen at higher magnification to branch between the non-branching, stacked prisms (Fig. 4).

Regularity and parallelism of prism course is generally regarded as a pleisiomorphic feature typical of multituberculates and some other mammals. Fosse et al. (1973) and Sahni (1979) have

noted the lack of prism decussation and the considerable bending of prisms towards the outer enamel in multituberculate incisors. Lack of decussation of prisms is now taken as an indication of a lack of independent (programmed) movement of parent ameloblasts (Boyde, 1969). The complexity of the pauciserial, multiserial and uniserial arrangement of prism course in rodent enamels (Korvenkontio, 1934-35; Wahlert, 1968; Sahni, 1980; von Koeningswald, 1980; 1985) is known to be exhibited early in the evolutionary process and is thought to have developed in the Palaeocene (Wahlert, 1968; Boyde, 1969; Sahni, 1980). On the other hand, non-cuspal marsupial enamel, again with the exception of the wombat (Beier, 1981; Ferreira et al., 1985; von Koeningswald, 1985), is generally described as non-decussating and with little zone formation (Tomes, 1906; Kawai, 1955; Boyde, 1969).

Yalkaparidon coheni, therefore, is quite marsupial-like in the simplicity of incisor prism course and quite unlike any so far described fossil rodent enamel; although the incisor could perhaps be interpreted as a theoretical model for a primitive proto-rodent, if such were to exist, prior to the development of the characteristic layering and cross-over of prisms. The proposal of von Koenigswald et al. (1987) that the prominent development of Hunter-Schreger bands in rodent incisors suggests a relationship between their presence and chewing stress helps serve to emphasize the "pre-rodent" nature of the incisor enamel described here.

Enamel tubules

Enamel tubules are found in extinct (Osborn and Hillman, 1979; Sahni, 1984; 1985) and living reptiles (Cooper and Poole, 1973); in multituberculates (Fosse et al., 1973; Osborn and Hillman, 1979; Sahni, 1984; Krause and Carlson, 1986; Sahni and Lester, 1988); all known marsupials except the wombat (Tomes, 1849; Mummery, 1924; Boyde and Lester, 1967; Lester et al., 1987a) and in a variety of other non-placentals. In placentals, enamel tubules have been described as occurring in variable degree in certain orders of Rodentia (Tomes, 1849; Von Ebner, 1890); Insectivora (Tomes, 1849); Chiroptera (Loher, 1929; Boyde, 1964; Lester and Hand, 1987); Cetacea (Ishiyama, 1984); and Ungulata (Boyde and Lester, 1967; Kozawa et al., 1981). For the majority of placentals, however, where tubules occur, they are few and restricted in extent to the very first formed enamel.

In considering Yalkaparidon coheni enamel in placental-marsupial terms, we were initially quite puzzled by the lack of clearly identifiable tubules in the fractured enamel surfaces of the incisor because it is generally accepted that within Theria the widespread occurrence of tubules is a major differentiating characteristic for marsupial enamel - for details see Tomes (1849), Boyde and Lester (1967), Lester et al. (1987a), Sahni and Lester (1987). We were reassured by the definitive identification of some few tubules close to the enamel-dentine junction and within the first 30 µm of enamel in the sectioned incisor material and the consistent presence of tubules in the premolar. Nevertheless, the relative lack of tubules in the incisor caused us to re-examine a number of living and fossil marsupial enamels available to us in order to assess relative differences, in very qualitative terms, between tubule presence in anterior as against posterior teeth.

We examined an enamel sample from an incisor of Diprotodon optatum; Zygomaturus trilobus; Palorchestes parvus; Thylacoleo carnifex and Ngapakaldia tedfordi. We found no tubules in Diprotodon optatum and Ngapakaldia tedfordi; very few small tubules near the enamel-dentine junction in Thylacoleo carnifex; tubules in the inner one third only of Zygomaturus trilobus; and numerous tubules in Palorchestes parvus. An enamel sample from a molar of Diprotodon optatum; Ngapakaldia tedfordi; Namilamadeta snideri; Protemnodon sp.; a wombat (a modern vombatid) and from a premolar of an unnamed Riversleigh marsupial was also examined. Tubules were found in all except the wombat: this is interesting in view of Tomes' (1849) original observation on the wombat and the interpretation of Namilamadeta snideri as a plesiomorphic sister group of the Vombatidae (Rich and Archer, 1979).

Of the living marsupials we have examined, only Tarsipes rostratus has shown a similar lack of tubules in the anterior teeth. We assessed by SEM in polished, etched sections the enamel from a functional lower incisor, a "non-functional" upper incisor, and a canine. No tubules were found in any of these teeth. Enamel from a molar, however, did show very occasional tubules in the inner one-third (Fig. 16). It is worth noting at this point that Tarsipes rostratus has atypical enamel for a marsupial in another significant respect: the upper incisor, canine and molar all display Pattern 1 prism packing with separated, complete round prisms up to 4 µm in diameter (Fig. 16), and the lower incisor displays very thin non-prismatic enamel (Fig. 17).

We would be the first to wish this aspect of enamel ultrastructure (the relative presence of tubules) to be put on a more quantitative basis at a SEM level and hope eventually to do so. Our present and early indications are, however, that when the fossil record is more fully examined, it may well show that Australian marsupial enamel in incisors at least was not always characterized by the presence of enamel tubules, at least to a degree any greater than that in many placentals. For the moment, our findings do little more than tantalize.

In conclusion, there is nothing in the enamel ultrastructure of the teeth of Yalkaparidon coheni that would suggest it being other than a fossil marsupial as proposed by Archer et al. (1988b) although in its combination of distinctive features it exhibits no particular affinities to any other order of marsupials. The salient features are: the Pattern 2 prism packing arrangement except at the thin and outermost prism-free zone; the parallelism and simplicity of rod course and the lack of real zone formation in a transverse plane; and the abundance of tubules in the premolar and their relative lack in the incisor. It must be said at the same time that a taxonomic interpretion based on the enamel ultrastructure of the incisor alone would be very confusing. The point is made because of the

possibility of significant variations in the enamel of anterior and posterior marsupial teeth: significant variation in prism course in the macropodoids is already known (Gilkeson and Lester, 1987; Lester et al., 1987a). It follows that the need for sampling of both anterior and posterior teeth for any one genus is important, although it is acknowledged that, especially for fossils, both simply may not be available for destructive examination.

It is becoming increasingly clear that a comprehensive catalogue of quantitative information is required if enamel ultrastructure is to be utilised in a meaningful way as an analytical palaeontological tool. It is also obvious that the application of various generalized but valuable morphological measures (for example, prism packing pattern) becomes difficult with the inherent differences in arrangement of components in fossil enamel, more specifically the greater inter-prism distance. There is, however, enough information already on hand to suggest that the vigorous application of morphometry to the prime features of prism diameter, shape, course and packing and of tubule location, size and density will yield valuable comparative data of considerable phylogenetic significance (e.g., Krause and Carlson, 1986, 1987). Mammalian fossil data are sufficiently rare and valuable in Australia to justify every effort in their analysis.

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Discussion with Reviewers

M. Ishiyama: I am very interested in the prismatic structure shown in Fig. 17. I have found a similar configuration in the enamel of the porpoise Neophocaena phocaenoides . Is the "aprismatic" structure of the enamel in Tarsipes rostratus "pre-prismatic" from a phylogenetic point of view?
Authors: This is likely to be a secondary, degenerative condition as you have suggested for Neophocaena phocaenoides (Ishiyama, 1987). Firstly, the teeth of this animal are conspicuously degenerate in terms of gross morphology, the I_1 being relatively reduced (in comparison to other diprotodontian marsupials) and the cheek teeth being reduced to mere spicules. Secondly, albumin MC'F serology, as well as some aspects of soft tissue morphology, provide clear indications that tarsipedids are most closely related to acrobatid possums which are themselves undoubted members of the suborder Phalangerida in the Order Diprotodontia, all other members of which appear to have prismatic enamel. Aplin and Archer (1987) have accordingly classified the tarsipedids as tarsipedoids, a superfamily of diprotodontian marsupials that also contains the Acrobatidae.

L. Moss-Salentijn: Enamel "spindles" in human enamel are extensions of the dentinal tubules, across the dentino-enamel junction. Thus, they seem to fit the presently accepted description of enamel tubules in marsupial enamel, with the difference that their number and size is much reduced in the human enamel. It has been a common observation that spindles are most numerous and largest in the cuspal enamel of human molars and premolars, while they are poorly represented in human incisors and canines. The findings in the present paper brought to mind the possibility of homology between spindles and enamel tubules. I wonder if the authors wish to comment on this.
Authors: We have always maintained, from our ultrastructural data, an ameloblastic origin to the normal, ordered, enamel tubules we find in the bulk of marsupial enamel (e.g., Lester, 1970; Lester et al. 1987a). We have acknowledged, at the same time, the necessary inter-relationship of the odontoblastic processes and the prospective ameloblast at the forming enamel-dentine junction region in order to provide the necessary dentine/enamel continuity (Lester, 1970). Spindles in human enamel and tubules in marsupial enamel are of an entirely different order of size, different in shape and, apart from their mutually transversing the enamel-dentine junction, different in distribution and extent. There must be at least a degree of homology between spindles and tubules developmentally, but we would see the odontoblast as by far the major or sole contributor to the spindle and the ameloblast as the major or sole contributor to the tubule.

G.Fosse: Lester et al. (1987a) stated that enamel tubules are present only in prism cores. Is that consistent with Fig. 13 where some tubular openings are situated in the inter-row sheets as well as at the border zone towards the prisms?

Authors: You are quite correct. As we study more marsupial enamels by SEM we increasingly observe a minority of tubules in extra-prismatic locations. Tubule course, however, remains a true reflection of the general path of the ameloblasts during enamel development: the cells relating in an integrated way and being responsible as they withdraw for the various phases we recognise in the completed enamel (prisms, inter-row sheet, and inter-prism).

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