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EVOLUTIONARY ASPECTS OF REPTILIAN AND MAMMALIAN ENAMEL STRUCTURE

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Abstract

The evolution of enamel structure is dealt with here on the basis of fossil reptiles and mammals ranging from the Triassic to the present. The evidence suggests that prismatic enamel had developed in some therapsid reptiles and the mammal, Eozostrodon about 180 million years ago. For the next 100 million years, mammalian evolutionary history is sparingly documented and this is reflected in the poor record of enamel evolution during this period. The few Jurassic reptiles and mammals studied suggest a pre-prismatic structure. In the Late Cretaceous (80 to 65 million years ago) when the fossil record improves, mammalian enamel investigated from North American localities, are found to be prismatic; allotherian (multituberculate) and metatherian (marsupial) enamels are usually tubular, while eutherian (placental) ones are not. Prism structure in Tertiary mammals in general, conforms to that of their present day descendants, but there are discernible exceptions. The record of evolutionary change in Tertiary mammals is obscured by functional modifications related to biomechanical stresses. Enamel structure may be secondarily modified; similar in phylogenetically unrelated groups (eg., pauciserial enamel of early rodents) or dissimilar at the intra-familial level (eg., rodent families Ctenodactylidae and Ischryomyicae). Prismatic enamel is recorded from the tooth of a hatchling of the gavial, Gavialis gangeticus.

KEYWORDS: Fossil reptile, mammal, Enamel evolution, geochronological distribution, prism patterns and structure.

Introduction

The present paper focusses attention on the evolution of mammalian enamels based principally on the evidence of fossil vertebrates. This aspect involves not only the documentation of the stages leading to the development of prismatic enamels, but also the study of the structural diversity of recent reptiles and mammals. While the prism packing patterns of extant reptiles and mammals has become better understood through the works of Cooper and Poole (1973) and Boyde (1964), there is still a lacuna with regard to the fossil record. During the last decade, considerable attention has been paid to the enamel structure of fossil-based evolutionary lineages, particularly those concerning the Rodentia, Cetacea and Primates. This has largely become possible because of a multidisciplinary approach involving palaeontologists and dental histologists, and the growing awareness that enamels of fossilized mammals have an excellent potential for documenting structural diversity on a scale much larger than that known for living mammals. Furthermore, all previous studies have shown that fossilized mineralized tissue undergoes negligible diagenetic alteration through time and faithfully records the prism structure, even in animals that are more than 200 million years old.

The pioneering efforts of Poole (1956, 1957) and Moss (1969) in studying fossil material by light microscopy have recently been taken up world-wide by several workers using scanning electron microscopy (Fosse et al. 1973, 1978, 1985; Carlson and Krause 1985; Koenigswald 1980; Boyde and Martin 1984; Kozawa 1984; Sahni 1979). While this has led to a better documentation of the enamel structure of diverse fossil organism, these studies have mainly been descriptive accounts of prism patterns and have lacked a theoretical model to interpret evolutionary mechanisms. There are still several unsolved issues that preclude a better understanding of the evolutionary processes in various recent and fossil organisms. Some of these points are discussed below.

Correspondence of phylogenies based on enamel structure and gross dental morphology

Many workers have emphasized the value of enamel structure in establishing phylogenetic relationships (Fosse et al. 1978; Carlson and Krause 1985; Flynn 1982; Koenigswald 1980; Boyde and Martin 1984). In general, the prism packing patterns follow taxonomic relationships established by evolutionary biologists. Primate, proboscidean, carnivore and taenioloabidoid multituberculate enamel are characterized by a predominance of Pattern 3 prisms, but their enamel ultrastructure is clearly distinguishable even in small samples. The ungulates (both artiodactyls and perissodactyls) are characterized by Pattern 2 prisms along with the marsupials. Amongst all mammalian orders, the rodents represent the most unified group on the basis of enamel ultrastructure even though there are sharp and distinct differences in enamel at the subordinal level. The great variety of prism arrangements at various taxonomic levels hinders, in many ways, the delineation and record of phylogenetic lineages.

Though precise correspondence at lower taxonomic levels is usually lacking, there is a general congruity between evolutionary lineages based on enamel ultrastructure and those based on dental or cranial characteristics. This aspect is particularly true of the condition prevailing in the multituberculates at the subordinal level (Carlson and Krause 1985) and agrees well with the situation prevailing in the Rodentia and the Primates, the only two other mammalian orders that have been studied in any detail in this regard.

Rodents are at present one of the best studied examples of such a conformity: the two extant rodent enamel patterns, the multiserial (most hystricognaths) and the uniserial (myomorphs and sciuromorphs) are clearly derivable from the pauciserial condition of the Early Tertiary rodents (Sahni 1980, 1984, 1985). When examined in greater detail, however, obvious discrepancies are seen to arise: the pauciserial condition is found in all Early Tertiary rodents even within those families, for instance the Ctenodactylidae and the Ischyromyidae which in the latter part of the Upper Tertiary acquired a multiserial and a uniserial enamel structure, respectively. The abruptness of this change from the pauciserial to the extant rodent enamel conditions may either be a signature of inadequate palaeontological sampling during the Oligo-Miocene, or may reflect modifications of the muscle stresses generated in the cranial and mandibular structure of hystricomorphous and sciurognathous rodents. Wilson (1972) postulated that the changeover to the uniserial condition preceded the modifications of jaw musculature, a viewpoint supported by Emry and Thorington (1982) on the basis of their study of Protosciurus, the most ancient squirrel known. Wood (1980, 1985), on the other hand, considered that the changing muscle tensions brought about the transition of the multi and uniserial enamel structure.

Similarly for the primates, Boyde and Martin (1982, 1984) have demonstrated a subordinal or superfamilial distinction as far as the enamel structure of fossil and Recent primates is concerned.

Structure in relation to function

The adaptive response of enamel structure at the crystallite and prism pattern level to such biomechanical stresses generated by crown size, hypsodonty, rootless conditions, leading and trailing wear margins, and lophodonty is only now becoming better understood (Koenigswald 1980; Fortelius 1984; Rensberger and Koenigswald 1980). This aspect is important because functionally related changes in the enamel structure may be lost or reintroduced several times in phylogenetic lineages and tend to obscure the main evolutionary trends of a particular lineage. Such modifications are not only significant at gross levels, but also at levels of resolution by electron microscopy.

With the exception of some hypsodont arvicolid rodents, in which the molar teeth are also rootless, the structure of the incisor is usually different from that of the molars. This differentiation can first be observed in the incisors of the ptilodontid multi tuberculate Mesodma (Sahni 1979). The structure of the rodent incisor has been studied in better detail as it has been considered to be of great taxonomic utility (Korvenkontio 1934). According to Koenigswald (1980), the acquisition of multiserial Hunter-Schreger bands in the incisors of various phylogenetically unrelated forms; Vombatus (Marsupialia); Daubentonia (Primates); Myotragus and Hippotragus (Artiodactyla); and in the hystricomorph rodents is a functional adaptation.

Materials and Methods

The material on which the present study is based was obtained from several sources:- Professor RE Sloan, University of Minnesota at Minneapolis, provided a generous sample of the Bug Creek Anthill micrommals of Late Cretaceous age. These include the multituberculates, Mesodma, Cimexomys, Meniscoessus, Stygimys and Catopsalis; the marsupial, Alphadon; the insectivores, Cimolestes and Gypsonictop and the condylarthran, Protungulatum. Professor TK Roy Chowdhary of the Geological Studies Unit, Indian Statistical Institute, Calcutta, loaned samples of Triassic thecodonts and traversodontid cynodonts from the Gondwana Pranhita-Godavari Basin of peninsular India for enamel ultrastructure work. The other material investigated here is from the author's own collection through field trips made in the Subathu formation of the Jammu Himalaya (Lower to Middle Eocene), the Berwali Series of Kutch of the same age, the Neogene deposits around Pinjor (Siwaliks of Haryana) and Srinagar (Karewas of Kashmir).

Several micrographs of each taxon were taken at the Institut fur Palaontologie, Bonn, on a Cambridge S-4 Scanning Electron Microscope (SEM) instrument with facilities provided by Professor HK Erben, Director, and funding through a Fellowship of the Alexander Von Humboldt Foundation, West Germany. Additional work was undertaken at the SEM Laboratories, Centre of Advanced Study in Geology, Panjab University, Chandigarh, on a JEOL-JSM-25S.

The taxa include several isolated thecodont teeth; cynodont and dicynodont therapsids from the Gondwana Pranhita-Godavari Basins of peninsular India; uncatalogued isolated teeth of Eozostrodon from Pant, Wales, presented to the Museum of Geology, Panjab University; Late Cretaceous allotherians, metatherians, and eutherians from the Bug Creek Anthills of Montana; fossil ziphodont and recent crocodiles; rhinoceratoids, tapiroids, artiodactyls and archaeocetes from the Eocene of Kashmir and Kutch; Eocene ctenodactylids, African phiomyids, Siwalik murids, rhizomyids, and primates (adapids and ramapithecines); and Karewa arvicolids.

All fossil specimens were cleaned using an ultrasonic vibrator and then etched with 2% HNO_3 for 8 to 10 sec, or with 0.5 HCL for 3 to 5 sec and were immediately washed and cleaned in an ultrasonic vibrator to remove etching precipitates (salts of chloride, nitrate etc.) which tend to build up on prism boundaries and other less etched areas. Small specimens which had to be sectioned in a specific orientation were first embedded in an araldite-based plastic, heated in an oven for 12 hours at 40°C and then ground and polished as desired.

Evolutionary Aspects

Though descriptive accounts of various mammalian enamels are found in the literature for well over a century (Tomes 1849, 1850), one of the earliest to consider the evidence of the fossil record was Korvenkontio (1934). Thereafter, as interest in the subject gained ground, the evolutionary aspects were pioneered in large measure by Poole (1956, 1957, 1967) and Moss (1969). The work of Poole (1956, 1957) is especially significant as it sought to document the reptilian to mammalian enamel transition, not only by considering comparative amelogenesis in recent species of the two Classes, but also by taking into account the fossil material. The evolutionary features of enamel structure of diverse Mesozoic and Tertiary vertebrates were highlighted by Moss (1969) by optical microscopy, and reviewed by Osborn and Hillman (1979). Many of the observations made by Moss (1969) have been modified by studies on the SEM (Fosse et al. 1973, 1978; Sahni 1979).

Reptilian Enamels (Fossil and Recent)

Using optical methods, Poole (1956, 1957) demonstrated that normal reptilian enamel has a uniform, parallel orientation of the hydroxyapatite crystallites perpendicular to the developing surface. He postulated that prism formation in mammals resulted from prolonged occlusion, accompanied by greater enamel thickness, and the location of stress points (prisms) generated by masticatory activity. The non-prismatic condition was considered to be the typical reptilian condition until Cooper and Poole (1973) demonstrated the presence of Pattern I prisms in Uromastyx, an agamid lizard. Since then few other additional reports of prismatic reptilian enamel have been published (Grine et al. 1979; Buffetaut et al. 1986). The presence of Pattern I prisms in theropod dinosaur enamel from various widespread localities throughout the world (Upper Jurassic of Thailand; Early Cretaceous of Tunisia and the Late Cretaceous of Canada) has recently been recorded, (Buffetaut et al. 1986). These findings suggest that the distinction between reptilian and mammalian enamels is less obvious than was previously considered, and that the classical theory concerning the reptile-mammalian enamel evolution may have to be revised in the light of occurrence of prismatic enamel in some non-occluding, multireplacement dentitions. These aspects had previously been discussed by Grine (1978) on the basis of his studies on Diademodon and Eozostrodon.

Poole (1957) considered that the transition from the non-prismatic enamel structure of most reptiles to the prismatic condition of most mammals, to be a relatively simple step which can be accomplished by the greater deepening of the Tomes Processes. The fact that some reptiles do have a prismatic structure raises the question that what, if anything, do these reptiles have in common? Two factors, enamel thickness and wear through occlusion have been cited as important in the development of prismatic enamel. At present, the answer to this problem is difficult to determine: in Uromastyx, the prismatic structure was ascribed by Cooper and Poole (1973) to the specialized nature of the dentition which remains in occlusion in contrast to the condition in most multireplacement type reptilian teeth. However, there are certain exceptions to the general, and apparently rational, principle of Poole (1957) that thick enamelled, occluding dentitions promoted the development of prisms. Sahni (1985) pointed out that not all therapsids that have occluding dentitions have prismatic enamels. Similarly, if the report of prismatic enamel in crocodiles and theropod dinosaurs is correct, then the factor of occlusion is not a necessary prerequisite for the evolution of prismatic structure. Furthermore, the Jurassic mammals of the Family Docodontidae did not possess prismatic enamels even though their teeth have undergone wear by occlusion (Moss 1969; Fosse et al. 1985). At present no well documented data exists on this critical period of mammalian history even though our knowledge of Jurassic mammals has increased considerably (Lillegraven et al. 1979).

The enamel of a Triassic thecodont from the Pranhita-Godavari Basin is illustrated here (Fig. 1) to show the features characteristic of most fossil and recent reptilian enamels. The enamel is usually thin, with pronounced incremental lines running throughout the thickness of the enamel. In most prismatic enamels, the incremental lines are usually discernible in those areas (usually the external layer of interprismatic enamel) where prisms are not developed. Enamel tubules may or may not be present.

In crocodiles, even by optical methods, a wavy, non-parallel orientation of the hydroxyapatite crystallites was noticed by earlier workers and was termed "Saulengliederung" (Poole 1956). Kumar (1983) recorded prismatic enamel (Type One Prisms) in serrated tooth crocodiles (Cf. Pristichampsus) from the Subathu Formation of India. However, subsequent work on the material from the same locality showed that the majority of teeth assigned to Pristichampsus did not have prismatic enamels. No reason can be ascribed to this discrepancy except to comment that different types of crocodiles may have been sampled which are impossible to differentiate on the basis of isolated material. In this connection, it is interesting to note the discovery of prismatic alligator enamel made by Y Dauphin (Lab. Paleontologie, Paris VI University, pers. comm. E Buffetaut).

The presence of prismatic enamel was observed in the extremely thin enamel of the tooth of a few day old hatchling of the gangetic gavial, Gavialis gangeticus, (Fig. 2). The specimen was obtained from the Kukrail Crocodile Farm, Lucknow, in connection with a project dealing with morphometry of developing crania of those crocodiles that had died prematurely. The teeth for study were dissected out of a skull having a length of 8.5 cm.

The enamel has a uniform thickness ranging from about 45 to 60 μm. Prisms are represented by circular, cylindrical rods, traversing the whole thickness of the enamel (Fig. 2). The differentiation into interprismatic and prismatic phases is quite distinct. The structure is extremely simplified and resembles that known for Uromastyx. No enamel tubules have been observed. It should be noted that a large sample of gavial hatchlings could not be obtained subsequently for detailed study as the species is on the National Conservation List. Furthermore, only certain transverse and sagittal sections showed the prismatic structure. In other sections the structure was not clear either as a result of preparation, artefact, or variation within the teeth. In adult teeth of Gavialis, both fossil and recent, the prismatic structure could not be observed.

Therapsids are mammal-like reptiles that developed a number of mammalian features by the end of the Triassic period. Their dentition, therefore, deserves special attention as this group of animals may hold the key to the problem of prismatic enamels. Although a number of genera have been studied by means of light microscopy (Moss 1969; Osborn and Hillman 1979) as well as by electron microscopy (Grine 1978; Grine et al. 1979; Sahni 1985), the enamel stucture is not well understood. There appears to be a wide structural range from tubular, non-prismatic, pre-prismatic and prismatic enamels (Pattern 1 prisms). Grine et al. (1979) demonstrated the existence of prisms in the South African therapsid repile, Pachygenelus, while Tritylodon was found to be non-prismatic. In an earlier study the related transversodontid Diademodon was also shown to be non-prismatic (Grine 1978). Similarly, Sahni (1985) found prismatic structure in Indian traversodontid cynodonts, which are presently generically indeterminable because the studied sample was comprised only of isolated teeth (Fig. 3). The traversodontids are associated with 2 dicynodont genera known from the Triassic of peninsular India, namely Wadiasaurus and Rechnisaurus (Chatterjee et al. 1969).

At present, there are no detailed studies on preprismatic (pseudo prismatic) enamel, even though this transitional phase was one of the most important in the evolution of enamel. In view of the uncertain interpretation of pre-prismatic enamel by light microscopy (Moss 1969; Osborn and Hillman 1979), only those fossil specimens will be mentioned that have been studied by electron microscopy.

The Haramiyidae whose affinities to both the reptiles and mammals are as yet uncertain, have been studied for their tooth enamel structure by Frank et al. (1984). The teeth referable to the genera Thomasia and Haramiya are small, cuspate, occlusally worn, and are considered to be ancestral to the multituberculates. Scanning electron microscopy of these Late Triassic teeth suggests a preprismatic structure. A similar condition was noticed in the Early Jurassic therian Kuehneotherium (Sigogneau-Russell et al. 1984). In another recent study on the microstructure of multituberculate enamel, Fosse et al. (1985) also investigated the teeth of primitive therians, including the plagiaulacoids and the docodontids. These mammals were also found to possess preprismatic enamel.

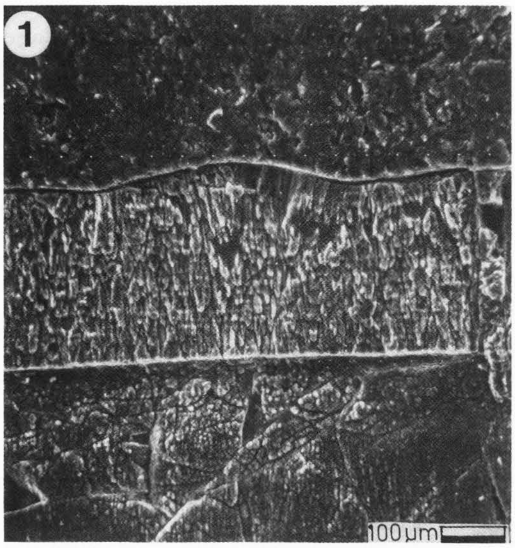
The report of prismatic enamel in Eozostrodon (Grine and Cruickshank 1978) is significant in the context of its geological antiquity and suggests that in eotherians, prism structure evolved at the same time as the development of mammalian dental structure. The structure of Eozostrodon enamel as described by Grine and Cruickshank (1978) has been confirmed by Sahni (1985).

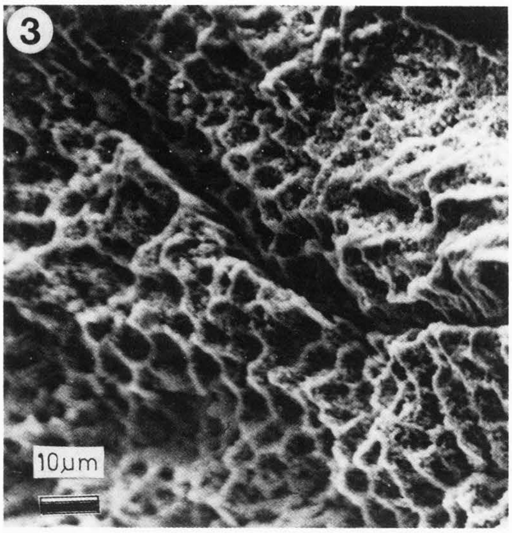
Mammalian Enamels

The best sampled primitive mammals are those from the Bug Creek Anthills of Montana from the Late Cretaceous. These enamels, which were contemporaries of the dinosaurs, had already differentiated into 3 well established subclasses: Allotheria (multituberculates), Metatheria (marsupials) and Eutheria (placentals). All these groups are represented by diverse genera with a herbivorous, omnivorous or insectivorous diet. The placentals were represented by the Orders Insectivora, Condylarthra and Primates.

Cretaceous

The characteristics of multituberculate enamel have been comprehensively studied by several workers, the latest account being that of Carlson and Krause (1985) and Fosse et al. (1985) and the reference contained therein. Basically, multituberculates have distinct prism patterns at the subordinal level: the Ptilodonoidea are represented by small-sized Pattern 1 prisms similar in many respects to contemporary eutherian enamels of Cimolestes and Gypsonictops except for the fact that ptilodontoids have tubular enamel. The Taeniolabioidea, on the other hand, are characterized by larger (prism diameters greatest known for all mammals) pattern 3 prisms, also with numerous enamel tubules. Sahni (1985) had suggested that in some taeniolabidoids, such as Stygimys, the prism structure may not be strictly homologous to Pattern 3 known in some living mammalian Orders. However, this suggestion has still to be examined in greater detail. Pattern 2 prisms form a small component in multituberculate enamels. Layering is not a common feature of most multituberculates, but it is a distinct feature of





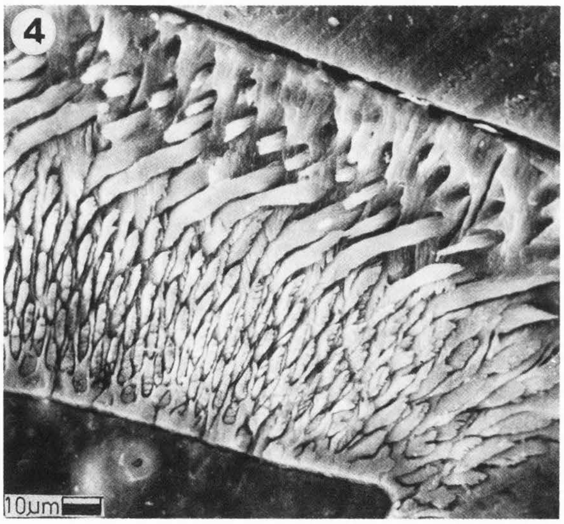


Fig. 1. Transverse section of Triassic thecodont tooth, Gondwana of Pranhita-Godavari Basin, peninsular India; enamel with prominent incremental lines.

Fig. 2. Sagittal section of tooth enamel of gavial hatchling showing differentiation into cylindrical rod-like prisms and interprismatic areas.

Fig. 3. Section showing enamel-dentine junction with circular prisms in Triassic traversodontid cynodont from the Gondwana of Pranhita-Godavari Basin.

Fig. 4. Transverse section of Mesodma (Late Cretaceous ptilodontid multituberculate) showing layering and bending over of prisms as a first stage of differentiation (probably functional) between incisors and molars.

the incisor (Sahni 1979). Transverse sections of the incisors of Mesodma show layering with an inner zone of elongated prisms inclined incisally. This structure represents one of the first functional adaptations of the incisors to biomechanical stresses (Fig. 4). In rodents, though the structure is basically different, the layering and the incisal bending of the prisms is still retained. The multituberculates, which were the palaeocological counterparts of the rodents, share with the latter group the condition in which the incisor structure was far removed from that of the molars.

The presence of tubules in the enamel, particularly in the Taeniolabidoidea, has been noticed by all workers who have studied multituberculate enamel. These occur in the prismatic as well as in the interprismatic phases and are in direct continuation with the dentinal tubules.

No systematic study has yet been undertaken on the enamel of fossil marsupials apart from the work done on the light microscope (Moss 1969). Preliminary work done on the genus Alphadon from the Bug Creek Anthill Hill locality indicates a structure similar to that known for recent marsupials (Sahni 1979). However, detailed evolutionary trends must await further investigations.

Of the Bug Creek eutherians, the enamel structure has been worked out only for the insectivores Cimolestes and Gypsonictops and the condylarhran Protungulatum. The primate Purgatorius known from this horizon has yet to be investigated, (Sloan and Van Valen 1965). The Late Cretaceous insectivores seem to have undergone little modification in respect to their modern counterparts which have Pattern 1 prisms (Sahni 1979). Protungulatum, on the other hand, considered by consensus opinion to be ancestral to most ungulates, possesses both Pattern 1 and Pattern 3 prisms. The latter pattern can be observed in Fig. 5 where the roughly hexagonal markings corresponding to the secretory territories of the ameloblasts can be seen along with the open-sided prisms boundaries. This type of preservation is rather uncommon in the fossil record.

Tertiary and Recent

The Tertiary was a period of great radiation leading to the present diversity of mammals. The first systematic documentation of Recent mammalian ultrastructure was undertaken by Boyde (1964) who laid down the foundation of evolutionary studies of the enamel structure of modern eutherian lineages. A beginning has thus been made in recording enamel evolution in most mammalian orders (Kozawa 1984). Important aspects of documentation include the description of the prism structure and the functional responses of the enamel structure of Tertiary and Recent lineages wherever there has not been a radical structural modification.

Recently, a great deal of attention has been paid to primate enamel evolution, particularly in the context of primitive hominoids, (Gantt et al., 1977; Gantt 1980, 1983; Vrba and Grine 1978; Sahni et al. 1983; Boyde and Martin 1984). Preliminary findings by Boyde and Martin (1984) suggest that Pattern 1, found in all Lemuriformes, may be considered as the most generalized for all Primates, implying thereby that Pattern 2 and 3 enamels represent derived conditions within the order, and to distinguish the cercopitheoids within that suborder. The structure of a Miocene Siwalik adapid primate wih predominantly Pattern 3 packing is shown in Fig. 6.

Cetacean enamel evolution has been studied by Sahni (1981) and Ishiyama (1984). These studies suggest that in the Middle Eocene when primitive whales (archaeocetes) had large, functional and occlusally worn teeth, the enamel structure was clearly prismatic (Pattern 1) with a well differentiated Von Korff layer and distinct Hunter-Schreger bands (Fig. 7). Recent odonocetes, on the other hand, lack well developed zonation, but otherwise have a similar structure to the archaeocetes. Smaller odontocetes tend to have more mineralized, better developed prismatic enamel than the larger-sized toothed whales (Ishiyama 1984).

There are interesting functional implications involved in the evolution of the enamel of rhinoceroses and lophodont ungulates (Rensberger and Koenigswald 1980; Fortelius 1984). Rensberger and Koenigswald (1980) have shown that the Hunter-Schreger bands in some Early to Middle Eocene lophodont perissodactyls (eg., the rhinoceratoids) were oriented horizontally and underwent a full 90° reorientation as evolution progressed in this group. The vertical orientation of the Hunter-Schreger bands is considered to impart to the lophs greater resistance to wear. Similar conditions of functional adaptation have been described for other lophodont ungulates including the Miocene suid Listriodon (Fortelius 1984).

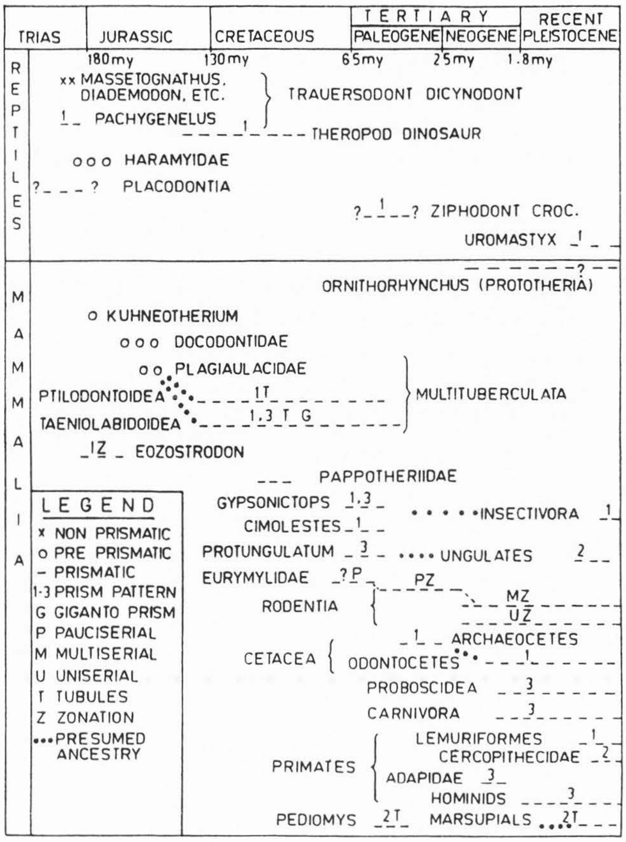
The record of enamel ultrastructure evolution in rodents is becoming clearer through the works of Koenigswald (1980, 1985), Sahni (1980, 1985), Hussain et al. (1978) and De Bruijn et al. (1982). The evolution in canid (Carnivora) enamels was undertaken by Reif (1974) while that in proboscideans by Kozawa (1978). The enamel ultrastructure of a Middle Eocene rodent and ungulate assemblage from the Lesser Himalaya of India was described by Kumar (1983).

The enamel structure of the prototherians is another fascinating subject which is just getting the attention that it deserves. Recently, Lester and Boyde (1986) have shown that Ornithorhynchus has prismatic enamel in part, but that this is not a primary feature of living monotreme enamel. Incremental lines and other radial features are more readily apparent. Lester and Archer (1986) in their study of the Middle Miocene monotreme Obduron have shown, on the other hand, that this taxon possesses prismatic tubular enamel. Pattern 1 predominates in the innermost enamel, while a Pattern 2 packing occurs in the middle third, the outermost enamel is non-prismatic. On the basis of the similarity of a number of enamel features between monotremes and multituberculates, these authors speculate on the possibility of a monphyletic origin for both these groups, a hypothesis which needs to be examined in greater detail.

Future Challenges

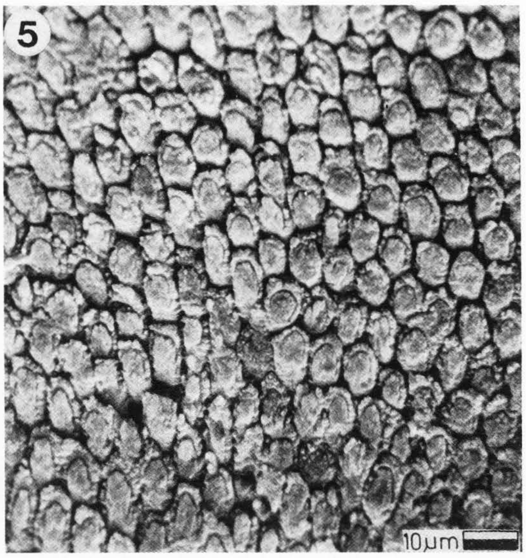
The interest aroused during the last decade in fossil vertebrate mineralized tissue has led to a better understanding of the taxonomic diversity and evolutionary significance of the dental histology of reptiles and mammals (Table 1). The future lines of investigation clearly fall into 3 categories:- first, to have a better understanding of the reasons (functional or otherwise) of the exception to the general enamel structure of a particular group; eg., the absence of tubules in Vombatus, the presence of a non-prismatic, tubular enamel in the cetacean Phoconoides, the loss of zones in most odontocetes, etc. Second, is the detailed documentation of enamel structure of those fossil lineages which are well established

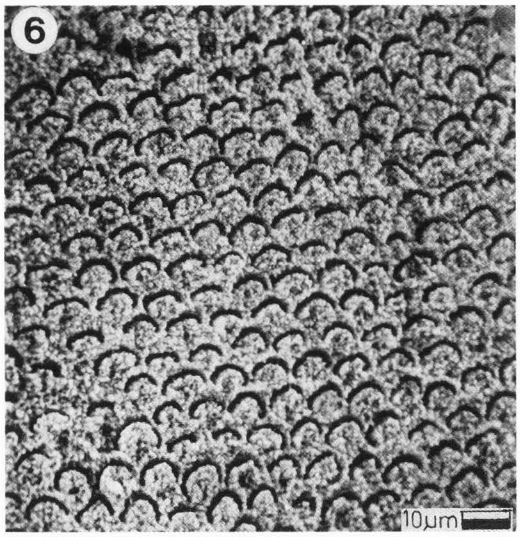
Table 1. Geochronological distribution of enamel structure in enamel of fossil reptiles and mammals.



on the basis of gross dental morphology and skeletal anatomy to analyse the reasons for similarities or discrepancies at the ultrastuctural level. Lastly, it is necessary to find out common factors for those reptiles that do possess prismatic enamels and for those mammals that do not.

The study of the evolution of enamel is still at the preliminary stage. Mesozoic reptiles and mammals hold the key in unravelling the complexities of enamel evolution.





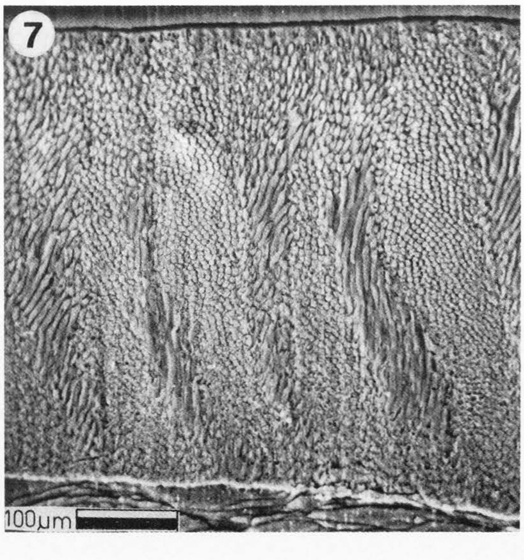


Fig. 5. Transversely sectioned enamel of Protungulatum (Late Cretaceous ancestral ungulate from Montana) showing Pattern 3 prisms.

Fig. 6. Horizontal section of the enamel of Sivaladapis nagrii (Adapidae, Primates, from the Indian Siwaliks) showing typical Pattern 3 prisms.

Fig. 7. Transverse section of enamel of primitive whale (Eocene archaeocete from Kutch, India) showing Hunter-Schreger Bands and Pattern 1 prisms. A differentiated Von Korff zone is present at the outer dentinal layer.

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Discussion with Reviewers

Reviewer III: There is a growing amount of controversy concerning discrete types of enamel structure, particularly relating to the categories: nonprismatic, preprismatic, pseudoprismatic. Can you, based on your work on specimen of taxa at your disposal, clarify this confusion?
Author: My observations are: some hatchling gavials did have prismatic enamel, others did not. The same applies to studies of fossil reptilian enamel where Buffetaut et al. (1986) found prismatic enamel in some theropod (carnivorous dinosaur) teeth from the Cretaceous of Canada, Jurassic of Thailand, etc. Also, Yannick Dauphine has recorded prismatic enamel in alligator enamel. I feel that these reports are significant and would motivate scientists to intensify their research along these lines. It is true that right now we do not fully know why some taxa have prismatic enamel and others do not.

Reviewer III: You state that multituberculates have Pattern 1 and Pattern 3 prisms. In your 1979 paper (p. 41), you state that "the principal arrangement of prisms conforms to Pattern 1 ... with a few oblique, horizontal and longitudinal sections showing Pattern 2. Contrary to findings of Fosse et al. (1973), Pattern 3 appears to be minimal or even absent". In your 1985 paper (p. 140), you refer to the prism arrangement in Stygimys, a taeniolabidoid, as "a modified version of Pattern 3," that is, it is not "strictly homologous to Pattern 3 prisms". Now, you refer to them as Pattern 3 prisms with no qualification or explanation of why they are not Pattern 2 or a modified Pattern 3. Which theory are we to believe?

Author: In 1979, when I published in Palaeontographica, there were very few papers on SEM application to fossil dental enamel. The dominant pattern that I recognized then for the multituberculates was Pattern 1 (with small amounts of Pattern 2). I failed to identify Pattern 3. In my 1985 paper (by which time a number of scientists had taken up this work and the general knowledge on the structure of fossil dental enamel was better), I revised my earlier opinion and considered both Pattern 1 and 3 to be the predominant patterns in the Ptilodontoidea and the Taeniolabidoidea, respectively.

Reviewer III: You list teeth of Eozostrodon as among those that were examined in the course of this study, yet no mention is made of Eozostrodon in the rest of the paper except to say that Grine et al. (1979) examined its enamel structure. Eozostrodon is crucial to our understanding of the early evolution of mammalian enamel. Did you find the same structure as did Grine et al.? You also list several other higher taxa that were apparently examined during the course of this study. What were your findings?

Author: Yes, I did find the same structure in Eozostrodon as reported by Grine and Cruickshank.